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SYSTEMATICS AND DISTRIBUTION OF CERATIOID ANGLERFISHES OF THE FAMILY CAULOPHRYNIDAE WITH THE DESCRIPTION OF A NEW GENUS AND SPECIES FROM THE BANDA SEA

By Theodore W. Pietsch

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The *Science Bulletin* and *Contributions in Science* of the Natural History Museum of Los Angeles County were merged into a single imperial octavo serial, retaining the name *Contributions in Science* and beginning with Number 301.

This serial has been newly formatted for maximum use of typography and illustrations per page, and sized for maximum use of paper. All photography has been produced utilizing a 200-line screen for detail.

Since most institutions rebind *Contributions in Science* collectively into hardbound volumes, and many researchers using them desire to photocopy material, two new features have been incorporated into the new format. A suggested citation line provides the abbreviated serial title, year, number of publication, and total pagination, and appears in the lower left corner of each page; and pages of *Contributions in Science* have been printed off-center to provide a two-inch gutter between adjacent pages for easier accessibility in photocopying.

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SYSTEMATICS AND DISTRIBUTION OF CERATIOID ANGLERFISHES OF THE FAMILY CAULOPHRYNIDAE WITH THE DESCRIPTION OF A NEW GENUS AND SPECIES FROM THE BANDA SEA[1]

By Theodore W. Pietsch[2]

ABSTRACT: The ceratioid anglerfish family Caulophrynidae is revised on the basis of all known material. The genus *Caulophryne* is represented by 26 female specimens collected from all three major oceans of the world. Of the six nominal species, three are recognized: *C. pelagica*, with *C. ramulosa* and *C. acinosa* as synonyms; *C. jordani*, with *C. regani* as a synonym; and *C. polynema*. A new caulophrynid genus and species is described from a single female recently collected from the Banda Sea. It differs from *Caulophryne* in having a considerably longer illicium, shorter jaw teeth, and a smaller number of relatively short median-fin rays. The tentative distribution of each species is plotted, evolutionary relationships are discussed, and a key to the genera and species of the family is provided.

This study supports a classification of the Ceratioidei in which the Caulophrynidae is the primitive sister-group of the Melanocetidae, Himantolophidae, Diceratiidae, Centrophrynidae, Oneirodidae, and Thaumatichthyidae. The position of the closely related families Linophrynidae, Gigantactinidae, and Neoceratiidae (and perhaps the Ceratiidae) is unclear. This assemblage is apparently derived either from a caulophrynid-like ancestor, forming a part of a sister-group that is primitive to all other ceratioids, or it is derived from some oneiroidid-like ancestor. In either case, it is concluded that sexual parasitism has evolved independently in at least two separate ceratioid lineages.

The ceratioid family Caulophrynidae includes globose, bathypelagic anglerfishes, easily distinguished from members of allied families by the absence of an escal bulb, the presence of two pectoral radials, extremely long dorsal and anal rays, and neuromasts of the acoustico-lateralis system located at the tips of elongate filaments. The only currently recognized genus of the family was established by Goode and Bean (1896) with the description of *Caulophryne jordani* based on a single female specimen with a parasitically attached male collected off Long Island, New York, by the Fisheries Steamer *ALBATROSS*. Since this original publication, five additional forms have been described, each from a single adolescent or adult female: *C. pelagica* (Brauer 1902); *C. polynema* Regan 1930; *C. ramulosa* and *C. acinosa* Regan and Trewavas 1932; and *C. regani* (Roule and Angel 1932). At the time of Bertelsen's (1951) monograph on the Ceratioidei the family was represented by only nine female specimens, one parasitic male, a male in metamorphosis, and 16 larvae. Not finding sufficient reason for subdividing this material into several species, Bertelsen (1951:37) provisionally recognized three subspecies: *C. jordani jordani*, representing a western North Atlantic subspecies; *C. jordani pelagica*, with *C. ramulosa* and *C. acinosa* as synonyms; and *C. jordani polynema*, including *C. regani* as a synonym.

The available material of *Caulophryne* represents three species: *C. pelagica*, represented by six female specimens collected from the eastern and Indo-west Pacific Ocean; *C. jordani*, by 11 females from all three major oceans of the world; and *C. polynema*, known from eight females and one attached male from the eastern Pacific and eastern Atlantic. The separation of these species is based on differences in dorsal and anal fin ray counts, tooth counts, illicium length, and illicial and escal morphology.

Despite a nearly three-fold increase in the number of known metamorphosed female specimens of *Caulophryne* since Bertelsen's (1951) revision, males are represented by only three individuals. Two of these are parasitically attached adults; the third is an unattached metamorphosis stage.

A new caulophrynid genus is also described in this paper and compared with *Caulophryne*. The single known female specimen of this new form is part of the extensive midwater collections made by Bruce H. Robison of the Marine Science Institute, University of California, Santa Barbara, during the 1975 *ALPHA HELIX* Southeast Asian Bioluminescence Expedition.

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METHODS AND MATERIALS

Standard lengths (SL) are used throughout. Measurements were taken from the left side whenever possible and rounded to the nearest 0.5 mm. To insure accurate fin-ray counts, skin was removed from the pectoral fins and incisions were made to reveal the rays of the dorsal and anal fins. Sockets, indicating missing teeth in the jaws and on the vomer, were included in total tooth counts. Jaw-tooth counts are the sum of both left and right sides. Head length is the distance from the anterior tip of the upper jaw to the posteriormost margin of the preoperculum. Head width is the distance between the tips of the sphenotic spines. Head depth is the distance from the tip of the sphenotic spine to the base of the quadrate spine. Lower-jaw length is the distance from the symphysial spine to the posteriormost margin of the articular. Illicium length is the distance from the articulation of the pterygiophore of the illicium and the illicial bone to the distal surface of the esca, excluding escal appendages. Lengths given for dorsal and anal rays are estimates of actual values since their distal portions are nearly always broken off.

Terminology used in describing the various parts of the angling apparatus follows Bradbury (1967). Definitions of terms used for the different stages of development follow Bertelsen (1951).

Locality data are presented for all specimens examined. Coordinates for the starting position only of each trawl are included. Most collections were made with an open, 3-meter Isaacs-Kidd midwater trawl (IKMT). Material deposited at the Institut für Seefischerei, Hamburg, was collected with a Combined Midwater Bottom Trawl, having a rectangular mouth and a 1600 mesh circumference (CMBT-1600). This and similar gear are described more fully by Schärfe (1966, 1969). Material from the Institute of Oceanographic Sciences, Surrey, England, was collected with a Rectangular Midwater Trawl, mouth area eight square meters, mesh size five millimeters (RMT 8/5), equipped with an opening and closing device (Clark 1969).

Material used for the osteological investigation (two female

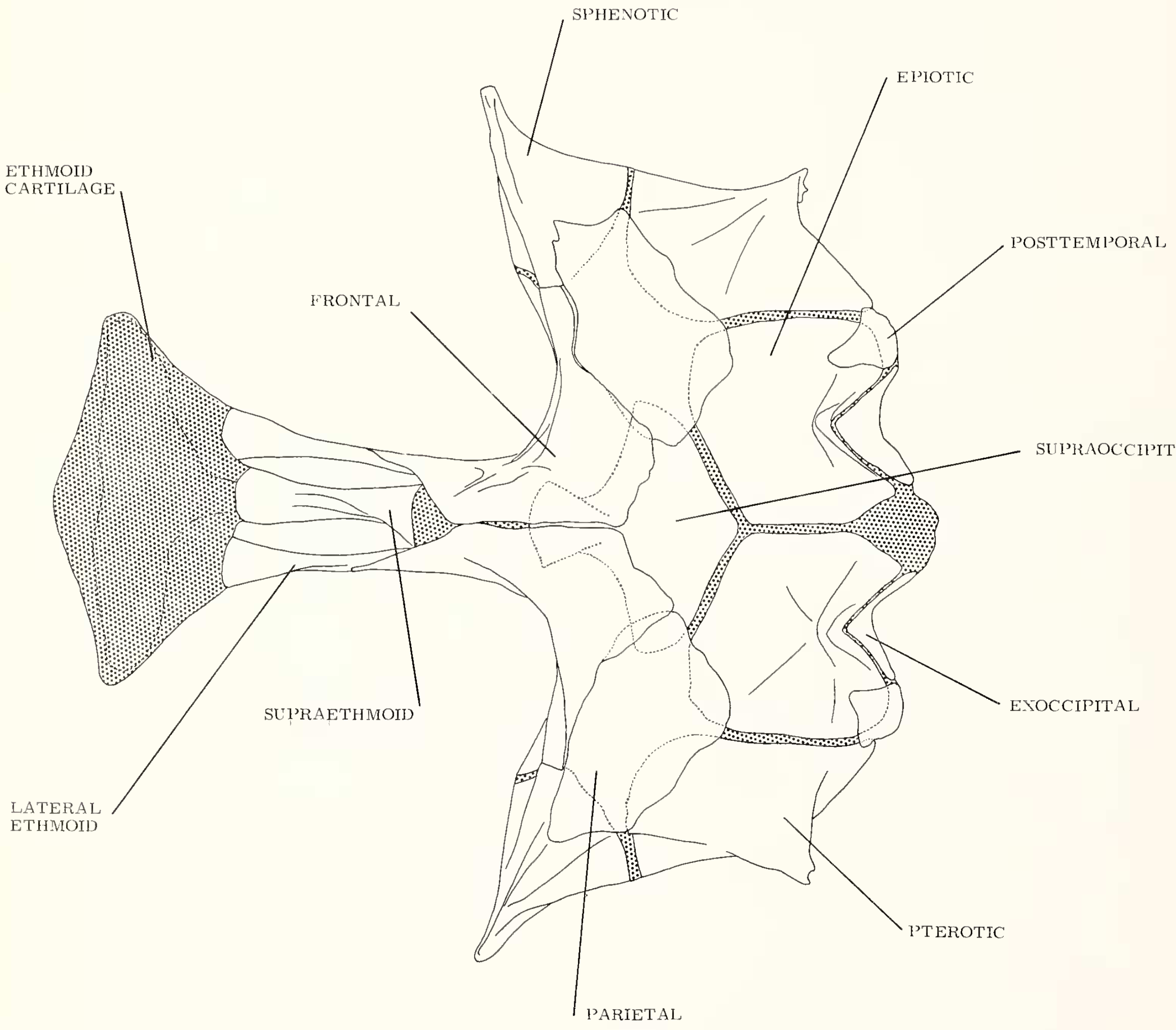


FIGURE 1. Dorsal view of cranium of *Caulophryne jordani*, IOS, 68.0 mm.

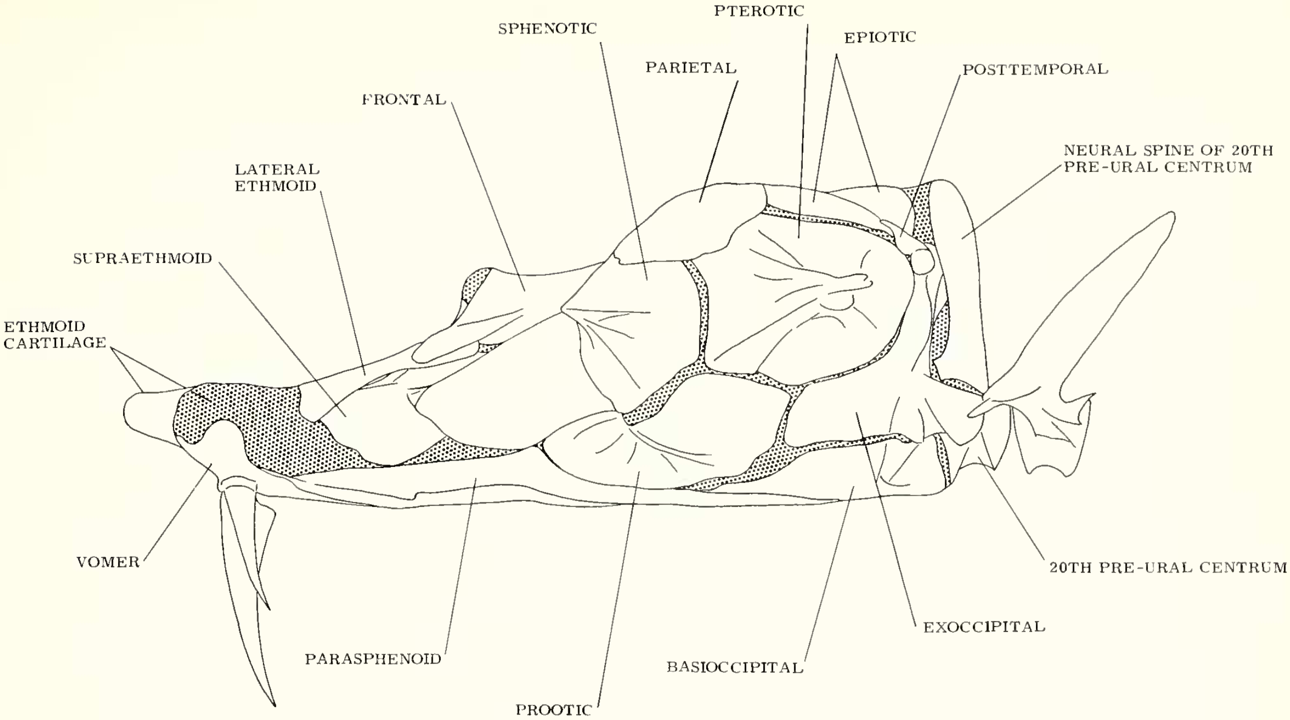


FIGURE 2. Lateral view of cranium of *Caulophryne jordani*, IOS, 68.0 mm.

Caulophryne jordani, 41.0–68.0 mm) was cleared and stained with alizarin red S following the trypsin digestion technique (Taylor 1967). In many cases dissections were made of uncleared specimens to confirm observations made on cleared and stained specimens and to determine ontogenetic changes. Bone terminology follows Pietsch (1972a) and Nybelin (1963). In osteological drawings cartilage is stippled, and where necessary for clarity, open spaces are rendered in solid black.

Unless otherwise indicated, all diagnoses and descriptions are based on females. For males and larvae see Bertelsen (1951:31–38). Material is deposited in the following museums and Institutions:

BMNH:	British Museum (Natural History), London.
IOAN:	Institute of Oceanography, Academy of Sciences of the USSR, Moscow.
IOS:	Institute of Oceanographic Sciences, Surrey, England (formerly the National Institute of Oceanography).
ISH:	Institut für Seefischerei, Hamburg.
LACM:	Natural History Museum of Los Angeles County.
MCZ:	Museum of Comparative Zoology, Harvard University.
MOM:	Musée Oceanographique de Monaco.
ROM:	Royal Ontario Museum, Toronto.
USNM:	National Museum of Natural History, Washington.
ZMB:	Zoologisches Museum der Humboldt-Universität, Berlin.
ZMUC:	Zoological Museum, University of Copenhagen.

OSTEOLOGY

Figures 1–13

The osteology of *Caulophryne* was partially described by Regan (1926:16, fig. 7), Regan and Trewavas (1932:42, figs. 56–58), and Bertelsen (1951:31, fig. 8). In the following account, only those comparative aspects that need amending or that have not previously appeared in the literature are discussed.

Cranium (Figs. 1–6): the ethmoid cartilage of *Caulophryne* broadly covers the dorsal surface of the vomer, extending beyond the margins of this bone on all sides. Anteriorly and laterally the head of the vomer turns upward to cup the ethmoid cartilage. The ventral surface of the vomer may bear as many as five, recurved and depressible teeth arranged in a transverse row.

In oneirodids (Pietsch 1974a:8, figs. 1, 4) the symphysial cartilage of the upper jaw butts up against a nearly vertical supraethmoid bone. In contrast, backward movement of the upper jaw of *Caulophryne* is limited by the lateral extensions of the vomer; an elongate, narrow groove is formed between the parallel lateral ethmoids and the obliquely placed supraethmoid providing space within which the small symphysial cartilage (see below) can slide. The anterior part of the pterygiophore (basal bone) of the illicium does not lie in this narrow groove as stated by Regan (1926:16).

The frontals are considerably shorter than those of oneirodids (Pietsch 1974a, figs. 1, 2). They meet on the midline for most of their length. Anteriorly, they contribute to the extremely narrow orbital region, overlapping the posterior ends of the lateral ethmoids; posteriorly they become greatly expanded laterally.

The parietals of *Caulophryne* occupy a more anterior position than in oneirodids, and are far removed from the posttemporals. Each is expanded laterally in an oblique position, overlapping four other bones: the sphenotic laterally, the pterotic and epiotic posteriorly, and the supraoccipital medially. Anteromedially, each parietal is slightly overlapped by the respective frontal bone.

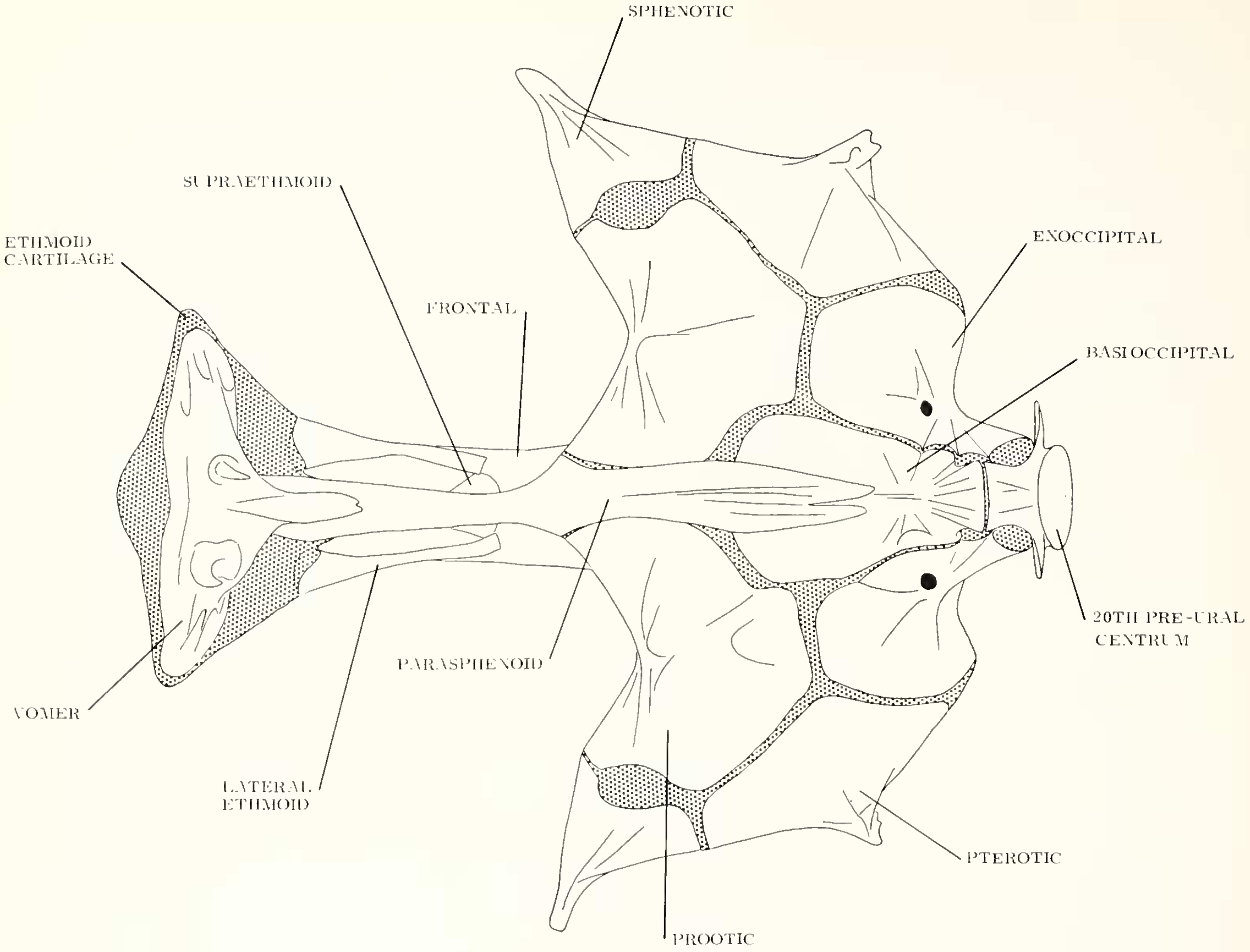


FIGURE 3. Ventral view of cranium of *Caulophryne jordani*, IOS, 68.0 mm.

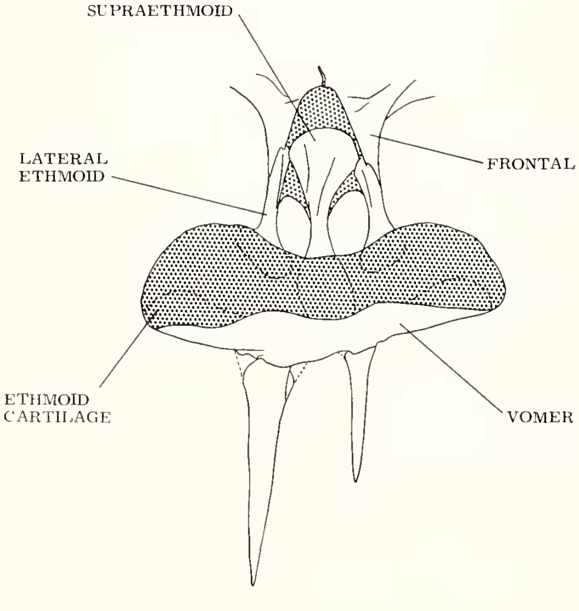


FIGURE 4. Anterior view of anterior half of cranium of *Caulophryne jordani*, IOS, 68.0 mm.

The pterosphenoid is absent (Pietsch 1972a:29).

Each sphenotic is a large, anterolaterally directed, cone-shaped element, the apex of which forms an elongate, blunt projection. On its ventral margin, each frontal, with the respective prootic bone, forms an oval-shaped cartilaginous area within which the anterior head of the double-headed hyomandibular articulates. The pterotic is also cone-shaped, but posterolaterally directed with a much larger base. A facet for the articulation of the posterior head of the hyomandibular bone is located ventrally at the apex of each pterotic.

In oneirodids (Pietsch 1974a:7, figs. 1–3) the prootics are separated anteriorly by the anteroventral process of the supraoccipital. In *Caulophryne* the supraoccipital maintains a dorsal position, largely overlapped anteriorly by the frontals, so that the prootics meet on the midline contributing to the formation of the posterior surface of the orbit.

Mandibular arch (Figs. 7, 8): Each premaxillary has a short articular process lying slightly behind and below an ascending process of similar size. Lying on the midline at the posterior tips of the ascending and articular processes of the premaxillae is a small, rounded symphysial cartilage loosely held by short ligaments and connective tissue. A postmaxillary process of the premaxillary is absent. The curved elongate portion of each premaxillary bears 12 recurved, depressible teeth of mixed sizes.

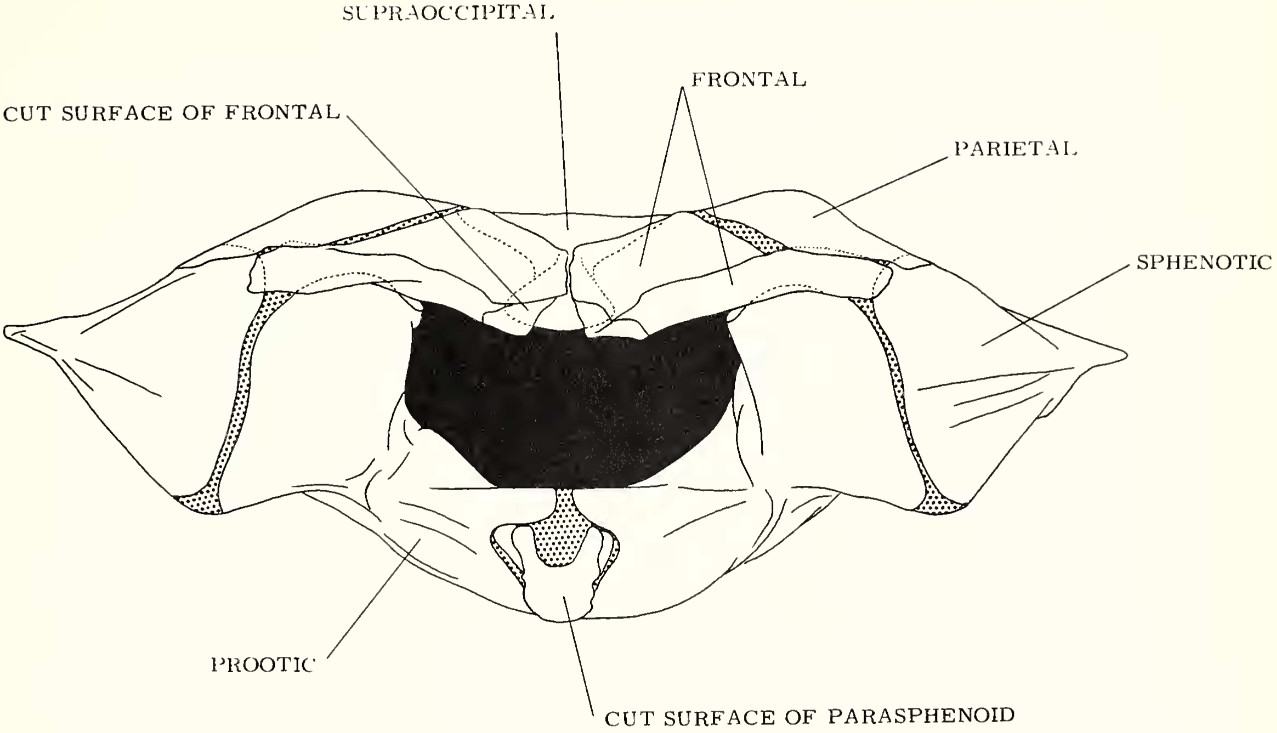


FIGURE 5. Anterior view of posterior half of cranium of *Caulophryne jordani*, IOS, 68.0 mm.

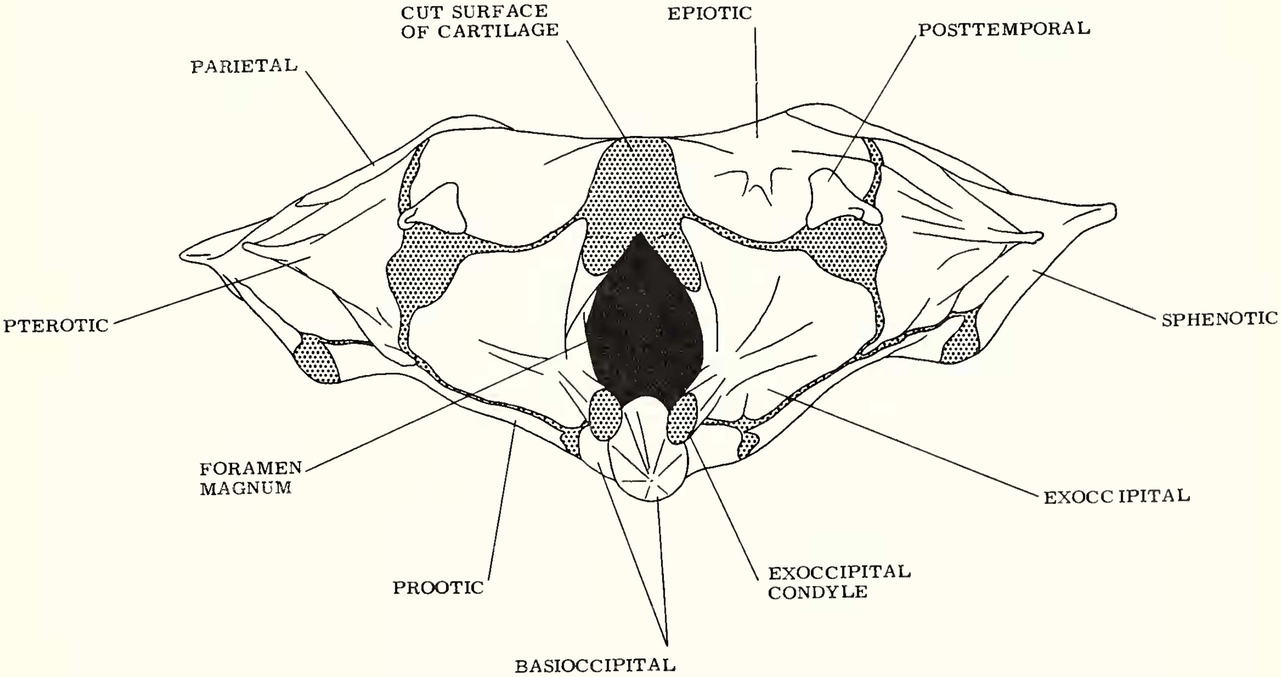


FIGURE 6. Posterior view of cranium of *Caulophryne jordani*, IOS, 68.0 mm.

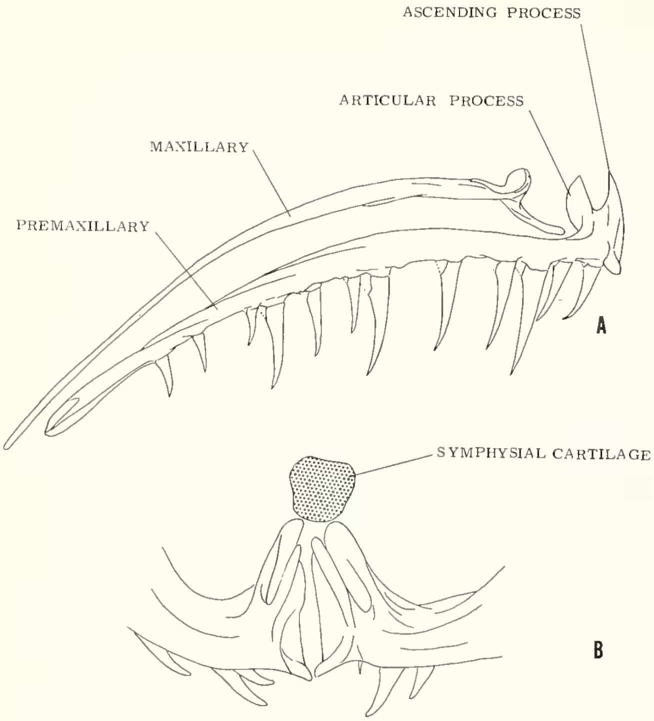


FIGURE 7. Upper jaw of *Caulophryne jordani:* A. IOS, 68.0 mm, lateral view of maxillary and premaxillary, right side; B. LACM 6844–3, 41.0 mm, lateral view of symphysis of premaxillaries showing symphysial cartilage.

The articular head of the maxillary consists of a slightly concave dorsal process which receives the anterior head of the double-headed palatine bone (see below), and a ventromedial projection which passes beneath, and provides support for, the premaxillary.

On each side, the posterior ends of the premaxillary and maxillary are united by a short ligament that passes posteriorly to attach to the ascending process of the articular. The anterior-maxillomandibular ligament (labial cartilage of Le Danois 1964; Pietsch 1972a:31), so well developed in oneirodids (Pietsch 1974a:9), is absent.

Anteriorly the dentaries curve to meet on the midline where they form a strong symphysial spine. The anterior half of each dentary bears nine to ten recurved, depressible teeth of mixed sizes.

Palatine arch (Fig. 8): The palatine arch is elongate and slender throughout. The anterior end of the palatine is T-shaped, consisting of a posterior head which is attached to the ethmoid cartilage, and an anterior head, which is loosely held within a shallow cavity of the dorsal process of the respective maxillary bone by connective tissue and by the palatomaxillary ligament. A narrow mesopterygoid is present but makes no contact with the metapterygoid.

Hyoid Arch (Figs. 8, 9): The suspensorium of *Caulophryne* is unusually narrow and elongate, and strongly directed obliquely backwards (compare with a typical oneirodid; Pietsch 1974a, fig. 8). The posterior head of the double-headed hyomandibular is the larger and longer of the two heads, forming a broad articulation with the pterotic. The anterior head of the hyomandibular articulates within a cartilaginous area formed between the sphenotic and prootic bones (the pterotic does not border on the articular area of the anterior head of the hyomandibular as it does in oneirodids; Pietsch 1974a:10, figs. 2, 3).

The greater length of the suspensorium, relative to other ceratioids (see above), is due largely to the extremely narrow, elongate quadrate. A large cleft is formed between the anterior and posterior portions of the quadrate within which lies the narrow ventral end of the symplectic. The interhyal is large compared to that of oneirodids (Pietsch 1974a, fig. 8).

The epihyal and especially the ceratohyal are narrow and elongate compared to those of oneirodids (Pietsch 1974a, fig. 9). In all but the most specialized lophiiforms (e.g., *Gigantactis, Neoceratias*) examined by me (Pietsch 1974a, Appendix B), the ceratohyal is notched anterodorsally to receive the posterior extension of the elongate, dorsal hypohyal (Rosen and Patterson 1969:439, fig. 57; Pietsch 1972a, fig. 14; 1974a, figs. 9, 10). In *Caulophryne* the anterodorsal notch is absent; the dorsal hypohyal is short and does not extend back over the dorsal surface of the ceratohyal. At midlength each ceratohyal forms a dorsal process that is securely attached to the anterolateral surface of ceratobrachial I by ligamentous connective tissue. A narrow ligament also extends anteriorly from the dorsal process of the ceratohyal to insert on the cartilage of the hypohyals.

The left ceratohyal of the 68.0 mm specimen (Fig. 9A) appears to be abnormally developed in having a deeply excavated posteroventral margin; together with the anteroventral corner of the epihyal, it supports only five branchiostegal rays: one anterior element (without an expanded head) on the inner side of the anterior, depressed portion of the ceratohyal, and four posterior elements (with expanded heads) on the outer surface of the elevated portion of the ceratohyal. The right ceratohyal (Fig. 9B) appears to be normally developed bearing six branchiostegals. Only one of these, however, is located anteromedially; five (all with expanded heads) are in a posterolateral position. Examination (by dissection) of all additional available material of *Caulophryne* showed the normal complement of six branchiostegal rays, two anteromedial elements, and four posterolateral elements. Previous to this, no lophiiform examined by me has had more than four posterior, laterally articulated branchiostegals; this number is considered diagnostic for the Paracanthopterygii as well as the Acanthopterygii (Greenwood, et al. 1966:353; Rosen and Patterson 1969:439).

Opercular bones (Fig. 8): The reduced operculum is bifurcated proximally forming two, extremely slender, and nearly parallel forks. The lower fork, more than three times the length of the upper, supports the suboperculum distally. The suboperculum is small, weakly-ossified (thought to be absent by Regan and Trewavas 1932:43, fig. 56), and deeply notched on its posterior margin. The large, posteriorly-curved preoperculum strengthens the entire length of the long hyoid arch extending dorsally along the posterior margin of the hyomandibular well past the point of the articulation of the operculum.

Branchial arches (Fig. 10): Pharyngobranchials I and IV are absent; those of the second and third arches are extremely well developed, bearing four to six recurved depressible fangs. Epibranchial I and ceratobranchial V are reduced, lying free in the connective tissue matrix. No ossified or cartilaginous remnants of hypobranchials or basibranchials could be found.

Vertebrae and caudal skeleton (Fig. 11): In the two cleared and stained specimens examined there are 20 vertebral centra (including the half-centrum to which is fused the hypural plate; Pietsch

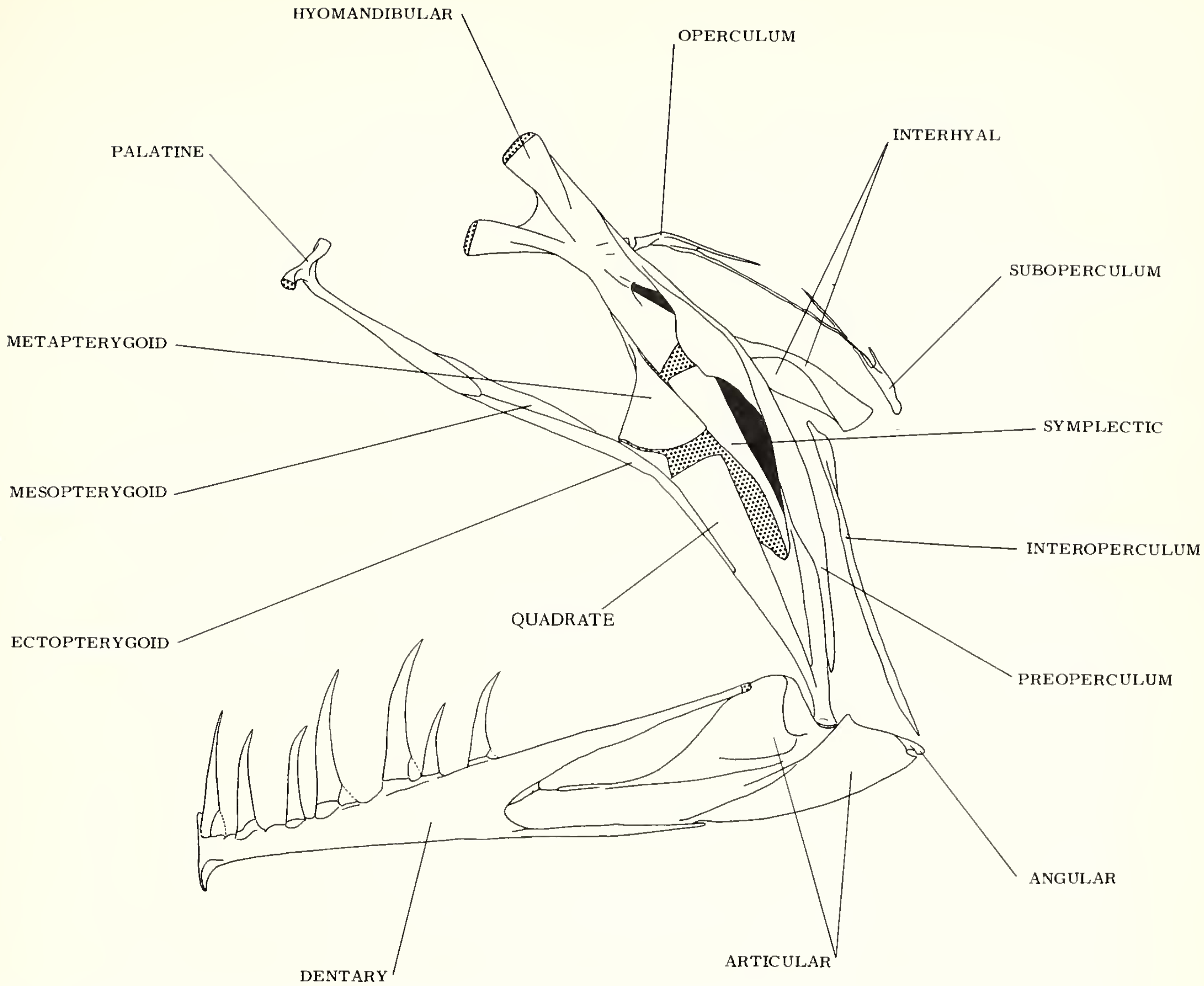


FIGURE 8. Lateral view of left side of lower jaw and suspensorium of *Caulophryne jordani,* IOS, 68.0 mm, with opercular bones in place.

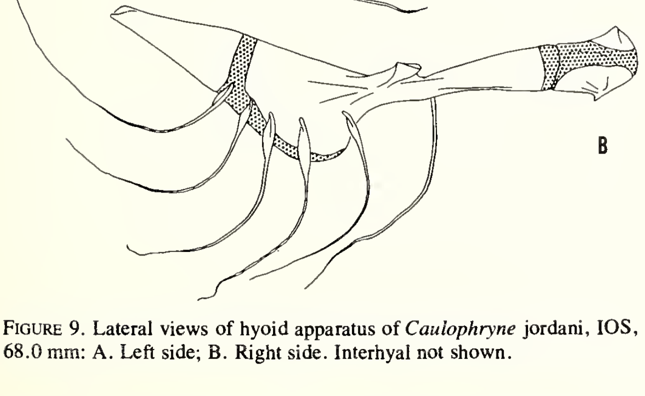


FIGURE 9. Lateral views of hyoid apparatus of *Caulophryne* jordani, IOS, 68.0 mm: A. Left side; B. Right side. Interhyal not shown.

1972a:38) of which ten or 11 are caudal vertebrae (those centra bearing complete haemal arches). There is a single, reduced epural (Pietsch 1972a:38). The hypural plate, deeply notched posteriorly in the larger cleared and stained specimen, but entire in the smaller specimen, bears the overlapping bases of eight principal caudal rays, the uppermost of which is exceptionally large. The central four caudal rays are bifurcated distally.

Median fins and illicial apparatus (Figs. 11, 12): The rays of the median fins are unusually long compared to other ceratioids, measuring, in extreme cases, more than twice the standard length. These rays are all biserial, segmented and unbranched, supported by elongate radials. In the 68.0 mm specimen there are 19 dorsal rays supported by 14 radials. The anteriormost radial supports the first dorsal ray and lies above the neural spine of the 12th pre-ural centrum. The posteriormost radial (which appears to be the product of two fused radials) supports the 14th and 15th dorsal rays and lies above the neural spine of the sixth pre-ural centrum. In the anal fin there are 17 rays supported by 14 closely associated radials. The anteriormost radial supports the first anal ray and lies below the haemal spine of the eighth pre-ural centrum. The posteriormost radial supports the 14th anal ray and lies below the haemal spine of the fourth pre-ural centrum.

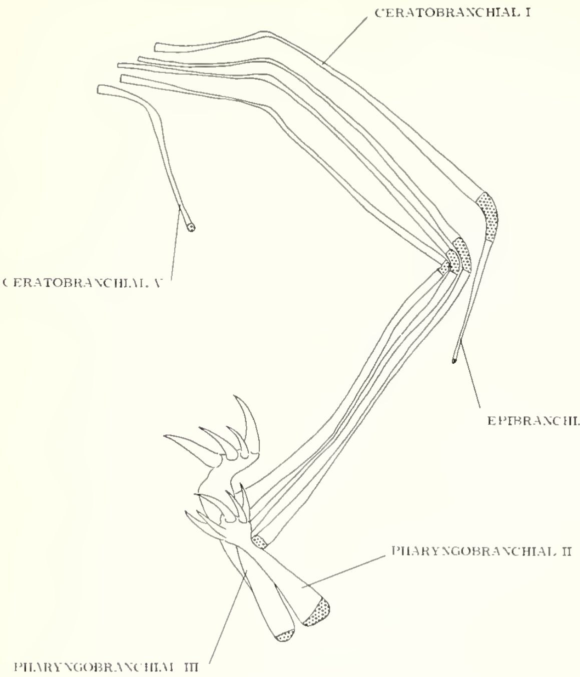


FIGURE 10. Branchial arches of *Caulophryne jordani,* IOS, 68.0 mm. The ventral part of the branchial basket is shown in dorsal view, the dorsal part (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

The pterygiophore of the illicium, excluding its downturned, cartilaginous posterior portion, is approximately 16 percent of standard length. The remnant of the second cephalic ray is a minute, toothlike ossification that lies on the pterygiophore just behind the articulation of the illicial bone. The length of the illicial bone varies slightly among *Caulophryne* species and becomes longer proportionately with growth (Fig. 16).

Pectoral girdle, pectoral fin, and pelvic bones (Fig. 13): The posttemporals of *Caulophryne* are small compared to those of other ceratioids. In oneirodids each posttemporal meets the respective parietal and overlaps the pterotic, epiotic and exoccipital (Pietsch 1974a:14, figs. 1–3, 5, 6). The reduced posttemporal of *Caulophryne* overlaps only the pterotic and epiotic being far removed from both the parietal (see above) and the exoccipital.

The supracleithrum of *Caulophryne* is unusually large covering most of the lateral surface of the upper portion of the cleithrum. The lower portion of the cleithrum is reduced to a slender, thread of bone.

The scapula consists of a rounded ossification bounded on three sides by cartilage. The posterior margin of the ossified part of the scapula supports the uppermost pectoral radial. The coracoid consists of an expanded dorsal portion which meets the cartilage of the scapula, an anteroventral process which is connected by a ligament to the reduced lower portion of the cleithrum, and an extremely large posteroventral process which meets the slen-

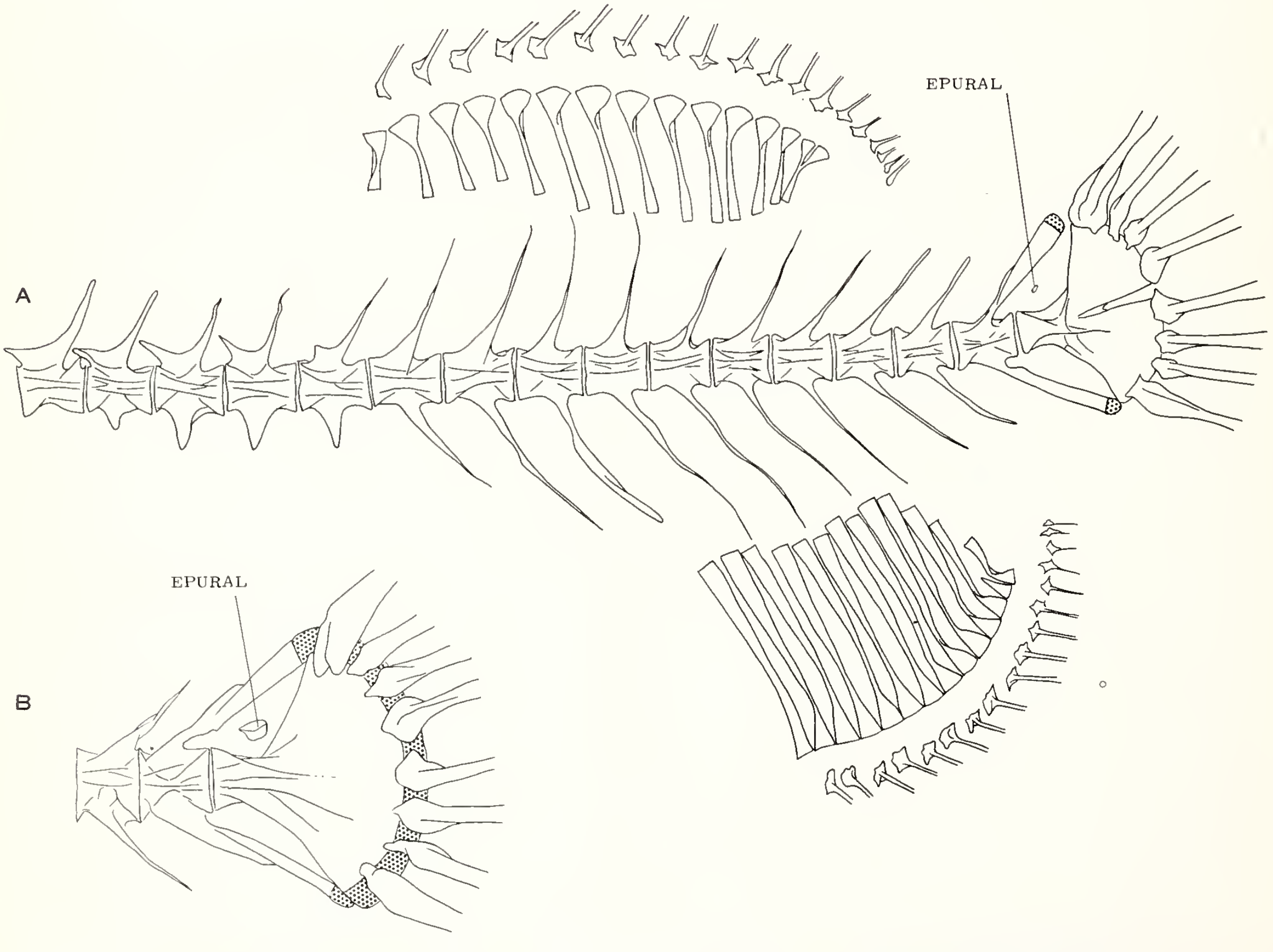


FIGURE 11. Vertebrae, caudal skeleton, and median fins of *Caulophryne jordani:* A. IOS, 68.0 mm; B. LACM 6844–3, 41.0 mm.

der postcleithrum distally.

There are two separate, well-ossified radials in fully metamorphosed specimens of *Caulophryne*, a small upper radial that bears no pectoral fin rays, and a much larger, distally expanded, lower radial that bears all the rays of the pectoral fin. The lower radial, however, is probably the product of two or more fused radials. A cleared and stained metamorphosing female (10.0 mm) clearly shows a deep, posterior cleft in the lowermost radial indicating at least three centers of ossification in the pectoral lobe (Fig. 13B). Fusion of pectoral radials appears to be common among ceratioids (Pietsch 1972a:41, fig. 23; Bertelsen and Struhsaker 1977).

Caulophryne is unique among ceratioids in the retention of pelvic fins in larval stages. Metamorphosis involves the loss of the pelvic fin rays but a pelvic bone is retained. The slender pelvic bones of *Caulophryne* lie free in the connective tissue matrix, far removed from the cleithrum. Unlike other ceratioids, these elements do not have cartilaginous distal tips.

Skin spines: Thorough microscopic examination of the skin of cleared and stained specimens failed to show the presence of embedded dermal spines.

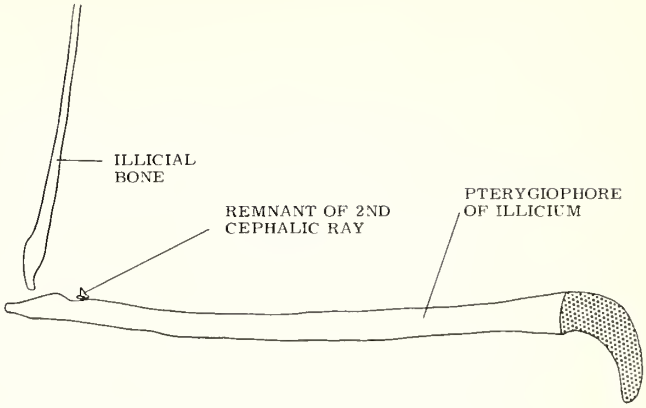


FIGURE 12. Illicial apparatus of *Caulophryne jordani*, IOS, 68.0 mm.

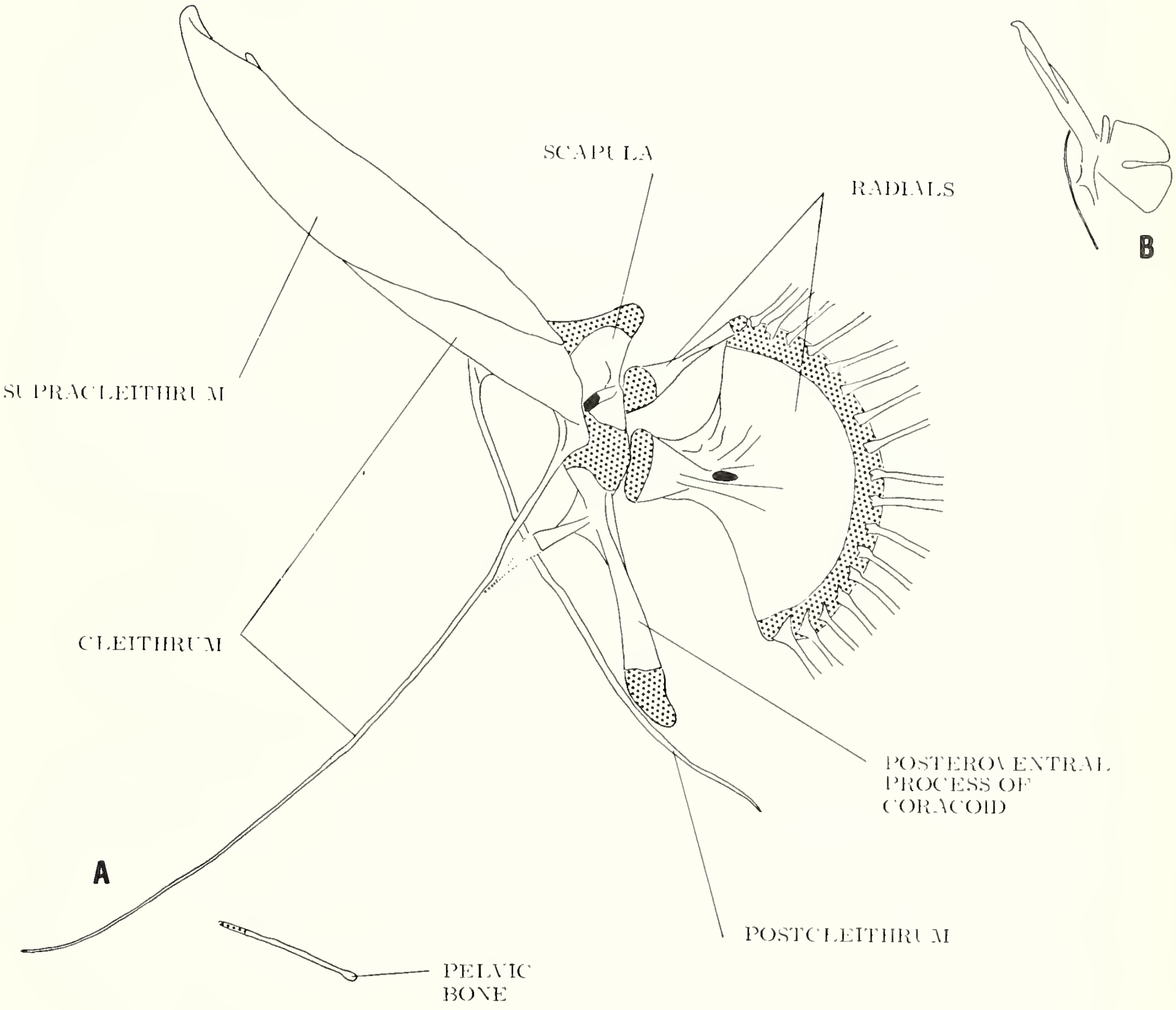


FIGURE 13. Lateral view of pectoral girdle, pectoral fin, and pelvic bone of *Caulophryne*: A. *C. jordani*, IOS, 68.0 mm; B. *C.* sp., IOAN, 10.0 mm.

SYSTEMATICS
Family Caulophrynidae Regan

Type genus *Caulophryne* Goode and Bean 1896.

Caulophrynidae Regan 1912:285, 288. Regan 1926:4, 16, 22. Regan 1930:195. Regan and Trewavas 1932:6, 14, 24, 25, 26, 42, 100. Roule and Angel 1933:55. Fowler 1936:1145, 1346. Belloc 1949:958. Bertelsen 1951:29, 31. Grey 1956:232. Monod 1960:684. Le Danois 1964:13, 14. Kobayashi, et al. 1968:8. Fitch and Lavenberg 1968:125, Fig. 69. Ueno 1971:102. Pietsch 1972a:18, 43, 45. Maul 1973:666. Pietsch 1976:783, 788, 791, 792.

DIAGNOSIS: The metamorphosed females of the family Caulophrynidae are distinguished from those of all other ceratioid families by having two pectoral radials, extremely elongate dorsal and anal rays, eight caudal rays, neuromasts of the acoustico-lateralis system located at the tips of extremely elongate filaments, larval pelvic fins, and the absence of an escal bulb. In addition, female caulophrynids share the following combination of characters: jaws equal anteriorly; supraethmoid present; parietals present, displaced anteriorly; pterosphenoid absent; anterior-maxillomandibular ligament absent (labial cartilage of Le Danois 1964; Pietsch 1972a:31); hyomandibular with a double head; 2 hypohyals; 6 (rarely 5) branchiostegal rays; operculum bifurcate, both forks reduced; suboperculum notched posteriorly, anterior spine or projection absent; pharyngobranchial I absent; epibranchial and ceratobranchial teeth absent; hypobranchials and basibranchials absent; a single, reduced epural; posterior margin of hypural plate notched in some specimens; only an ossified remnant of second cephalic ray present; posttemporal reduced; lower portion of cleithrum reduced; posteroventral process of coracoid well-developed; pelvic fins present in larvae; pelvic bones of metamorphosed females rod-like, not expanded distally; esca without denticles; skin spines absent.

DESCRIPTION: Body relatively short, globular (Figs. 14, 20); oral valve well-developed, lining inside of both upper and lower jaws; two nostrils on each side at the end of a single short tube; eye small and subcutaneous, appearing through a circular, translucent area of integument; gill opening oval in shape, situated just posteroventral to pectoral lobe; all four epibranchials closely bound together by connective tissue; posterior third of ceratobranchial I bound to ceratobranchial II; no opening behind fourth arch; gill filaments present on anterior-most tip of ceratobranchial I and full length of ceratobranchials II through IV; pseudobranch absent; pattern of placement of acoustico-lateralis system as described for other ceratioids (Pietsch 1969, 1972b, 1974a, b); neuromasts situated at the tips of elongate filaments; ovaries paired; two, short pyloric caeca.

Illicium becoming proportionately longer with growth (Fig. 16); anterior end of pterygiophore of illicium exposed, emerging on snout, its posterior end concealed under skin; esca unpigmented and translucent, simple, without elaborate appendages *(Robia)*, or consisting of several branched appendages or numerous filaments *(Caulophryne)*; escal bulb and central lumen absent; entire length of illicium covered with translucent filaments in some forms of *Caulophryne*.

Teeth slender, recurved and depressible, those in lower jaw less numerous, but slightly longer than those in upper jaw; number of teeth in lower jaw 14–34, in upper jaw 20–45; total number of teeth on vomer 1–5; pharyngobranchials II and III heavily toothed.

Color in preservative dark brown to black over entire surface of body (except for esca, and in some forms, the illicium) and oral cavity; viscera unpigmented.

D. 6–22; A. 5–19; P. 15–18 (Table 1); pelvics with 3–4 rays in larvae and metamorphosis stages, absent in adolescents and adults; C. 8 (2 unbranched – 4 branched – 2 unbranched).

The following measurements, expressed in percent of SL, are summarized for the females (20.0–142.0 mm) of all species: head length 27.2–41.7; head depth 32.7–45.4; head width 21.9–30.6; lower jaw 31.3–48.1; premaxillary 28.9–44.4; longest tooth in lower jaw 5.1–9.5; longest dorsal ray 63.4–155.3; longest anal ray 39.0–151.1; illicium 16.0–268.3.

Robia NEW GENUS

Type species: *Robia legula* new species.

DIAGNOSIS: The genus *Robia* is distinguished from *Caulophryne* (the only other member of its family) in having a considerably longer illicium (268.3 percent of SL), shorter jaw teeth,

Key to the Genera and Species of the Caulophrynidae

The following key will differentiate adolescent and adult female specimens only. Characters that allow specific identification of males (known from only three specimens, two of which are parasitically attached to females) and larvae (16 specimens; Bertelsen 1951:35, figs. 8, 11) are unknown.

1A. Illicium long, 268 percent of SL in a 41 mm specimen; D.6, A.5 .... *Robia legula* new genus and species (single known specimen, 41.0 mm).

1B. Illicium short, less than SL; D. 14–22, A. 12–19.......... *Caulophryne* 2

2A. Illicium with translucent filaments along entire length (Figs. 19, 21); length of illicium less than 35 percent SL (Fig. 16); D. 16–22, A. 14–19 (Table 1) 3

2B. Illicium without filaments (Fig. 17); length of illicium greater than 35 percent of SL (Fig. 16); D. 14–17, A. 12–16 (Table 1) .... *C. pelagica* (Brauer 1902).

3A. Upper jaw with more than 35 teeth in specimens larger than 40 mm, 30 or more in specimens larger than 20 mm (Fig. 18); illicium with more than 50 filaments along entire length in specimens larger than 32 mm (Fig. 21); D. 20–22 (rarely 19), A. 18–19 (rarely 17) (Table 1) .... *C. polynema* Regan 1930.

3B. Upper jaw usually with less than 35 teeth in specimens larger than 40 mm, less than 30 in specimens larger than 20 mm (Fig. 18); illicium with less than 15 filaments along length (Fig. 19); D. 16–18 (rarely 19), A. 14–17 (rarely 18) (Table 1) .... *C. jordani* Goode and Bean 1896.

TABLE 1
Frequencies of fin-ray counts for species of Caulophrynidae

Species	Dorsal										Anal									Pectoral			
	6	14	15	16	17	18	19	20	21	22	5	12	13	14	15	16	17	18	19	15	16	17	18
Robia legula	1										1											2	
Caulophryne pelagica		3	1		2							3	1		1	1				3	2	3	2
Caulophryne jordani				5	2	3	1							3	3	4		1			5	10	3
Caulophryne polynema							1	1	4	2							1	4	3	1	5	6	4
Total	1	3	1	5	4	3	2	1	4	2	1	3	1	3	4	5	1	5	3	4	12	21	9

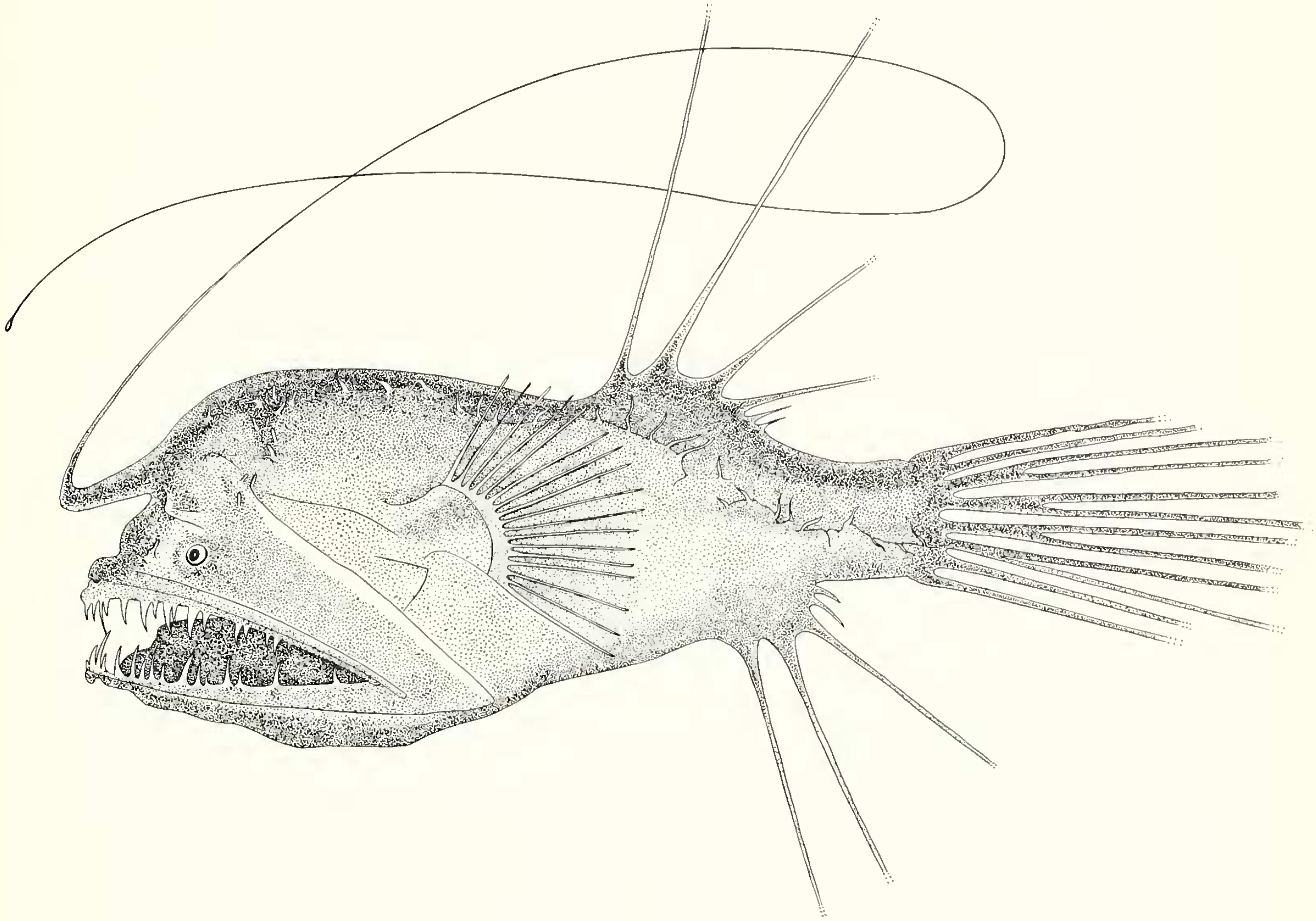


FIGURE 14. *Robia legula*, Holotype, LACM 36024-1, 41.0 mm. Drawn by Caryl Maloof.

and a smaller number of relatively short median fin rays (D.6, less than 65 percent of SL; A.5, less than 40 percent of SL).

ETYMOLOGY: The name *Robia*, to be treated as a noun of feminine gender, is given in honor of Bruce H. Robison (better known to his friends as "Robie") in recognition of his contributions to our knowledge of midwater fishes.

Robia legula NEW SPECIES

Figures 14, 15, 24

HOLOTYPE: LACM 36024-1, 41.0 mm; *ALPHA HELIX* Southeast Asian Bioluminescence Expedition Station 81, Banda Sea, 4° 56.5′S, 129° 59.5′E, RMT-8 with closing device, 1000-1500 m, 0416 - 0616 hr, 28 April 1975.

DESCRIPTION: Illicium without filaments, darkly pigmented along entire length except near esca; esca translucent, with two short lateral appendages and a slightly more opaque distal tip bearing three short appendages (Fig. 15).

Total number of teeth in lower jaw 31, in upper jaw 33; vomerine teeth 4; D. 6; A. 5; P. 17 (Table 1).

Measurements in percent of SL: head length 39.0; head depth 39.0; head width 23.4; lower jaw 47.6; premaxillary 37.8; longest tooth in lower jaw 5.1; longest dorsal ray 63.4; longest anal ray 39.0; illicium 268.3.

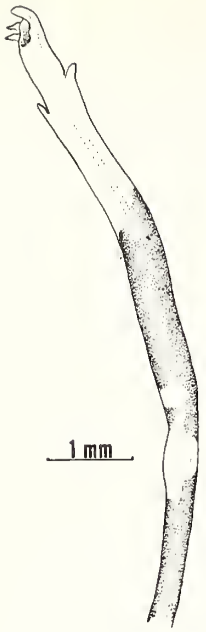


FIGURE 15. Esca of *Robia legula*, Holotype, LACM 36024–1, 41.0 mm.

Rest of characters as for genus and family.

DISTRIBUTION: *Robia legula* is known from a single specimen collected from the Banda Sea (4° 56.5'S, 129° 59.5'E) with an opening-closing trawl between 1000 and 1500 m.

ETYMOLOGY: The name *legula* is derived from the Latin *legula*, meaning collector or gatherer, alluding to the extraordinary collecting abilities of this anglerfish and its collector.

Caulophryne Goode and Bean 1896

Caulophryne Goode and Bean 1896:496, fig. 409 (type species *Caulophryne jordani* Goode and Bean 1896, by original designation and monotypy).

Melanocetus Brauer 1902:295 (in part; type species *Melanocetus johnsoni* Günther 1864, by monotypy). Brauer 1906:321, pl. 15, fig. 5 (after Brauer 1902).

Ceratocaulophryne Roule and Angel 1932:500 (type species *Ceratocaulophryne regani* Roule and Angel 1932, by monotypy). Roule and Angel 1933:55 pl. 3, figs. 26, 26A (after Roule and Angel 1932; expanded description).

DIAGNOSIS: The genus *Caulophryne* is distinguished from *Robia* (the only other member of its family) in having a considerably shorter illicium (less than 50 percent of SL), longer jaw teeth, and a greater number of relatively long median fin rays (D. 14–22, greater than 70 percent of SL; A.12–19, greater than 60 percent of SL).

Caulophryne pelagica (Brauer 1902)

Figures 16–18, 24

Melanocetus pelagicus Brauer 1902:295 (original description, single specimen). Brauer 1906:321, plate 15, fig. 5 (after Brauer 1902). Regan 1926:22 ("probably a synonym of *C. jordani*").

Caulophryne pelagicus Regan 1912:288 (new combination; listed).

Caulophryne jordani Regan 1926:22 (in part; specimen later described as *C. ramulosa* sp. n. by Regan and Trewavas 1932). Kobayashi, et al. 1968:8–12, figs. 1, 2, tables 1, 2 (additional specimen; description).

Caulophryne ramulosa Regan and Trewavas 1932:100, 101, pl. 7, fig. 160 (original description; single specimen, previously recorded by Regan 1926, as *C. jordani;* in key) Bertelsen 1951:36, 37, tables 2, 3 (description; a synonym of *C. jordani pelagica*).

Caulophryne acinosa Regan and Trewavas 1932:100, 101, pl. 8, fig. 161 (original description; single specimen; in key). Bertelsen 1951:36, 37, tables 2, 3 (description; a synonym of *C. jordani pelagica*).

Caulophryne pelagica Regan and Trewavas 1932:100, 102, fig. 162 (new orthography; in key; description after Brauer 1902, 1906, esca figured). Bertelsen 1951:36, 37, fig. 9, table 3 (figure after Brauer 1906; a subspecies of *C. jordani*).

Caulophryne jordani pelagica Bertelsen 1951:33, 37, fig. 9, table 3 (in key; description, comparison with all known material; includes *C. ramulosa* and *C. acinosa*). Grey 1956:233 (synonymy; after Bertelsen 1951). Kobayashi, et al. 1968:9 (new specimen most similar to).

MATERIAL: Six known females, 11.0 – 92.0 mm.

Holotype of *Melanocetus pelagicus:* ZMB 17711, 11.0 mm; *VALDIVIA* Station 228, Indian Ocean, 2° 38'S, 65° 59'E, 0–2500 m, bottom depth 3460 m.

Holotype of *Caulophryne ramulosa:* ZMUC P9245, 57.0 mm; *DANA* Station 1209(1), Gulf of Panama, 7° 15'N, 78° 54'W, 3500 m wire, 1845 hr, 17 January 1922.

Holotype of *Caulophryne acinosa:* ZMUC P9244, 19.0 mm; *DANA* Station 3920(2), Indian Ocean, 1° 06'S, 62° 25'E, 3500 m wire, bottom depth 4630 m, 1830 hr, 9 December 1929.

NONTYPE MATERIAL: LACM 30619–6, 65.0 mm; *VELERO* IV Station 9903, 29° 30'N, 118° 54'W, 3-m IKMT, 0–834 m, 2315–0515 hr, 7 August 1964. LACM 36023–1, 13.0 mm; *ALPHA HELIX* Southeast Asian Bioluminescence Expedition Station 143, 0° 14.5'S, 128° 46.7'E, RMT-8, 1250–1500 m, 1715–1930 hr, 20 May 1975.

Fisheries Museum, Faculty of Fisheries, Hokkaido University F-1639, 92.0 mm; No. 3 Shichisei Maru, 42° 40'N, 144° 40'E, 0–500 m, 0800–1200 hr, 26 April 1967.

DIAGNOSIS: In addition to differences in escal morphology (Figs. 17, 19, 21), *C. pelagica* may be distinguished from *C. jordani* and *C. polynema* in having a slightly longer illicium (Fig. 16), fewer dorsal fin rays (Table 1), and by the absence of illicial filaments (Figs. 17, 19, 21). It is further separated from *C. jordani* by having a greater number of upper jaw teeth (Fig. 18). *Caulophryne pelagica* probably also has longer median fin rays than its congeners, but this character is difficult to quantify accurately because the distal ends of the rays are nearly always broken off.

DESCRIPTION: Illicium without filaments, darkly pigmented along entire length except near esca; esca consisting of five or six elongate, filamentous appendages: two, more lateral in position, bearing none to several side branches, and three or four, more distal, bearing numerous side branches; opaque areas absent (Regan and Trewavas 1932:101, 102, figs. 160–162; Fig. 17).

Total number of teeth in lower jaw 24–34, in upper jaw 28–40 (Fig. 18); vomerine teeth 2–3; D. 14–17; A. 12–16, P. 15–18 (Fig. 18, Table 1).

Measurements in percent of SL; longest tooth in lower jaw 5.8–6.8; longest dorsal ray 105–228; longest anal ray 132–174; illicium 31.6–43.9 (Fig. 16).

Rest of characters as for genus and family.

DISTRIBUTION: *Caulophryne pelagica* is represented by two specimens collected in the Indian Ocean, a third record from the Halmahera Sea, East Indies (13.0 mm, collected with a closing trawl between 1250–1500 m), a fourth from off Guadalupe Island, Mexico, a fifth off Japan, and a sixth specimen from the

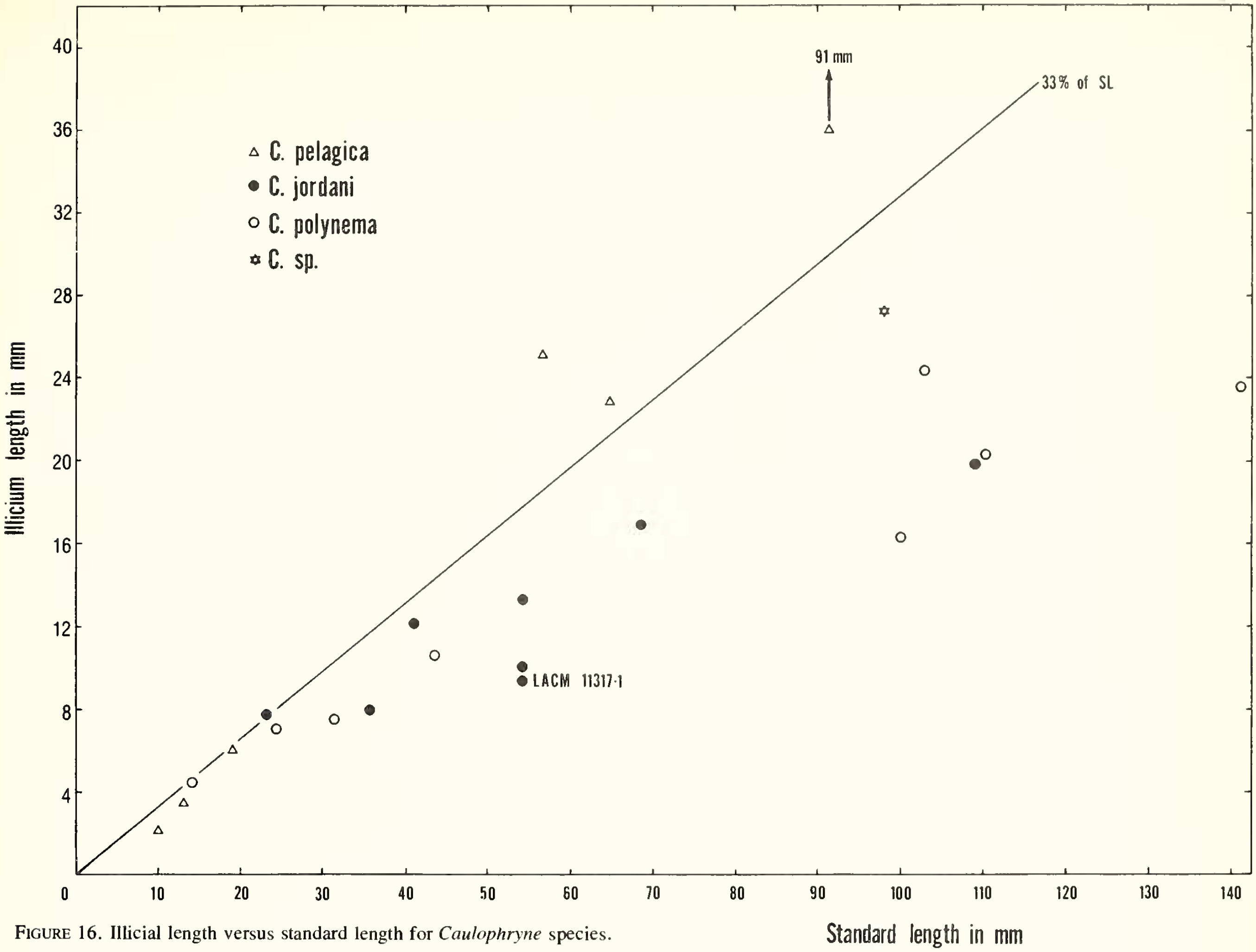
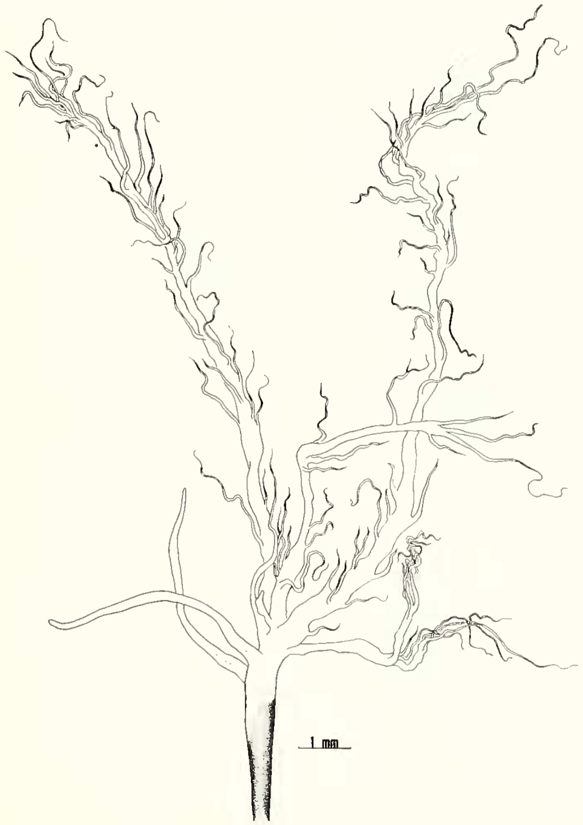


FIGURE 16. Illicial length versus standard length for *Caulophryne* species.



Gulf of Panama (Fig. 24).

COMMENTS: The results of this investigation confirm Bertelsen's (1951:36) opinion that *C. ramulosa* and *C. acinosa* are junior synonyms of *C. pelagica*. The illicia of the holotypes of all three are "well-preserved and constructed in a very similar fashion." Further, all three nominal forms agree in having a slightly longer illicium and fewer median fin rays than other species.

Caulophryne jordani Goode and Bean 1896

Figures 1–13, 16, 18, 19, 24

Caulophryne jordani Goode and Bean 1896:26*, 496, 541, fig. 409 (original description; single specimen; erroneous name in list of plates, index, figure caption). Jordan and Evermann 1898:2735 (description after Goode and Bean 1896). Jordan and Evermann 1900, fig. 957 (figure after Goode and Bean 1896). Gill 1909:586, fig. 24 (brief description and figure after Goode and Bean 1896). Regan 1912:288 (description after Goode and Bean 1896). Beebe 1926:422 (additional specimen). Regan 1926:4, 22, figs. 7, 16 (cranial osteology; expanded description). Beebe 1929:19 (additional specimen). Regan 1930:191, 193 (comparison with *C. polynema*). Regan and Trewavas 1932:6, 100, 101, fig. 159 (in key; brief description after Goode and Bean 1896; illicium figured).

← FIGURE 17. Esca of *Caulophryne pelagica*, LACM 30619-3, 65.0 mm.

Roule and Angel 1933:57 (comparison with *C. regani*). Bertelsen 1951:33–38, figs. 8–11, tables 2, 3 (description, comparison with all known material; three subspecies). Lavenberg and Ebeling 1967:195; fig. 5 (vertical distribution). Kobayashi, et al. 1968:8–12, figs. 1, 2, tables 1, 2 (additional specimen here referred to *C. pelagica;* description). Fitch and Lavenberg 1968:125–127, fig. 69 (distinguishing characters; natural history). Ueno 1971:102 (listed). Pietsch 1972a:29, 35, 36, 38, 41–43, 45, fig. 24(3) (osteology; otolith described, figured). Pietsch 1976:783 (reproduction).

Ceratocaulophryne regani Roule and Angel 1932:500 (original description; single specimen). Roule and Angel 1933:55–57, pl. 3, figs. 26, 26a (expanded description: figures of holotype, lateral, dorsal views). Belloc 1949:17 (listed). Bertelsen 1951:36, table 3 (a synonym of *C. jordani polynema*). Kobayashi, et al. 1968:8 (after Bertelsen 1951).

Caulophryne regani Fowler 1936:1347 (new combination; in key; description after Roule and Angel 1932, 1933).

Caulophryne jordani polynema Bertelsen 1951:33, 37 table 3 (in part; includes *C. regani* here referred to *C. jordani*). Grey 1956:233 (after Bertelsen 1951). Maul 1973:666 (after Bertelsen 1951).

Caulophryne jordani jordani Bertelsen 1951:33, 37, table 3 (in key; one of three subspecies; description, comparison with all known material). Grey 1956:232 (synonymy; after Bertelsen 1951).

MATERIAL: Eleven known females, 23.0–109.0 mm.

Holotype of *Caulophryne jordani:* USNM 39265, 26.0 mm; *ALBATROSS,* off Long Island, New York, 39° 27′N, 71° 15′W, 0–2335 m, 19 September 1887.

Holotype of *Ceratocaulophryne regani:* MOM Galerie: Level 3, Window 55, 38.0 mm; *HIRONDELLE II* Station 3279, west of the Azores, 38° 55′N, 34° 07′W, 0–3000 m, 23 August 1912.

NONTYPE MATERIAL: LACM 11317–1, 54.0 mm; *USNS ELTANIN* Station 1825, 39° 58′S, 160° 34′E, 3-m IKMT, 0–1625 m, 0218–0613 hr, 5 December 1966. LACM 33924–1, 54.0 mm; *VELERO IV* Station 17668, 32° 42′N, 118° 13′W; 3-m IKMT, 0–750 m, 0947–1505 hr, 28 June 1972. LACM 6844–3, 41.0 mm; *VELERO IV* Station 7325, 33° 36′N, 118° 24′ W, 3-m IKMT, 0–640 m, 1129–1420 hr, 9 March 1961 (cleared and stained).

IOS uncatalogued, 68.0 mm; *DISCOVERY II* Station 7480, 39° 55.2′N, 20° 07.4′W, RMT, 1250–1510 m, 0921–1321 hr, 7 November 1970 (cleared and stained). IOS uncatalogued, 36.0 mm; *DISCOVERY II* Station 8281–43, 31° 44′N, 63° 58′W, RMT-8, 1235–1260 m, 1358–1658 hr, 20 March 1973.

USNM 148469, ca. 75 mm; *ALBATROSS* Station 2530, 40° 53′N, 66° 24′W, 14 June 1885. USNM 216461, 54.0 mm; *OCEAN ACRE* Cruise 10, Station 21N, 31° 27′N, 64° 49′W, 3-m IKMT, 0–880, 1955–0135 hr, 6 June 1970.

ROM 27250, 109 mm; *BRANDAL* Tow 3, 50° 30′N, 49° 30′W, Engel Trawl, 0–1070 m, 0710–1000 hr, 12 July 1968.

MCZ 51279, 23.0 mm; *ANTON BRUUN* Cruise 6, Station 339B, APB 7231, 04° 14′S, 65° 02′E, 3-m IKMT, 0–275 m, bottom depth 3900 m, 0715–1610 hr, 30 May 1964.

DIAGNOSIS: In addition to differences in escal morphology (Figs. 17, 19, 21), *C. jordani* is distinguished from *C. pelagica* and *C. polynema* in having fewer upper jaw teeth (Fig. 18). The dorsal fin of *C. jordani* has a greater number of rays than that of *C. pelagica,* and fewer rays than that of *C. polynema* (Table 1). It is further distinguished from *C. pelagica* in having a slightly shorter, filamentous illicium; illicial filaments are absent in *C. pelagica,* but considerably more numerous in *C. polynema* (Figs. 17, 19, 21).

DESCRIPTION: Illicium pigmented except near esca, with 5 to 14 elongate (up to 87 percent of illicium length), translucent filaments along entire length, all but distal-most arising from posterior margin; esca with a posterolateral appendage bearing numerous short filaments and having a palmate (usually bilobed), opaque, distal tip; two distal appendages: the posterior-most slender, bearing numerous filaments, the anterior-most short and stout, opaque along posterior margin, and bearing numerous filaments (separation into two distal appendages not as evident in specimens less than 40.0 mm); and an elongate, filamentous, anterolateral appendage (illicial and escal filaments lost in holotype. see Regan and Trewavas 1932:101, fig. 159; Fig. 19).

Total number of teeth in lower jaw 16–26, in upper jaw 20–39; vomerine teeth 2–5; D. 16–19, A. 14–18, P. 16–18 (Fig. 18, Table 1).

Measurements in percent of SL: longest tooth in lower jaw 6.1–9.3; longest dorsal ray 78–115; longest anal ray 82–110; illicium 17.6–33.9 (Fig. 16).

Rest of characters as for genus and family.

DISTRIBUTION: *Caulophryne jordani* is known from all three major oceans of the world: seven records from the North Atlantic, one from the Indian Ocean, one from the Southern Ocean at approximately 40°S, 160°E, and two from off southern California. The two IOS specimens from the north Atlantic (36.0 and 68.0 mm) were collected with a closing trawl between 1235 and 1260 m, and 1250 and 1510 m, respectively (Fig. 24).

COMMENTS: The illicial apparatus of the holotype of *C. jordani* is somewhat damaged as indicated by a drawing provided by Regan and Trewavas (1932, fig. 159), and as noted by Bertelsen (1951:36). Filaments normally found along the length of the illicium and arising from the esca are absent. The posterolateral escal appendage and two distal appendages, however, remain intact. In these and all other characters the additional material (with a minor exception, see below) here assigned to *C. jordani* compares very well with the holotype.

Bertelsen (1951:37) believed that *Ceratocaulophryne regani* and *Caulophryne polynema* might be synonyms on the basis of similarity in illicial morphology, "position of the fins, and relative dimensions." This conclusion. however, is not supported by data provided by Jørgen Nielsen of the Zoological Museum, University of Copenhagen. In illicial and escal morphology, jaw tooth counts, and in dorsal and anal fin ray counts (16 and 16, not 15 and 14, respectively, as given by Roule and Angel 1933), the holotype of *C. regani* compares well with the material here recognized as *C. jordani*. *Ceratocaulophryne regani* is removed from the synonymy of *C. polynema* and placed within that of *C. jordani*.

The 54.0 mm specimen of *C. jordani* from the Southern Ocean (LACM 11317–1) differs from other individuals of this species in having a higher number of jaw teeth (Fig. 18).

Caulophryne polynema Regan 1930

Figures 16, 18, 20, 21, 24

Caulophryne polynema Regan 1930:191–195, figs. 1–3 (original description; single female specimen with parasitically attached male). Parr 1930:131, fig. 4 (figure after Regan 1930). Regan and Trewavas 1932:100, 101 (in key; description after Regan 1930). Fowler 1936:1347 (in key; description after Regan 1930). Bertelsen 1951:36, 37, fig. 12, table 3 (figure after Regan 1930; a subspecies of *C. jordani*). Pietsch 1976:789 (reproduction).

Caulophryne jordani polynema Bertelsen 1951:33, 37, fig. 12, table 3 (in key; description, comparison with all known material; includes

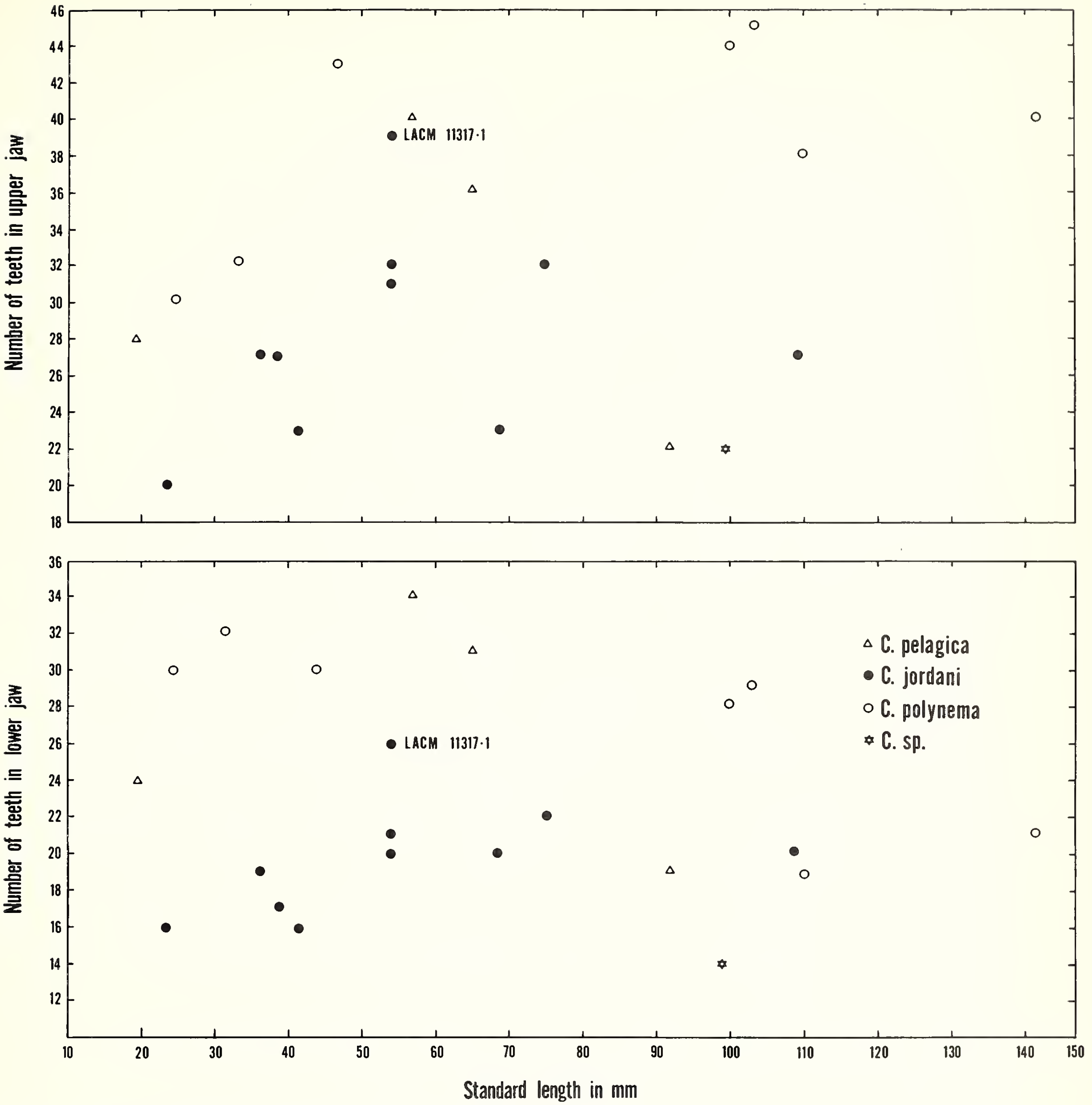


FIGURE 18. Number of teeth in upper and lower jaws versus standard length for *Caulophryne* species.

Ceratocaulophryne regani Roule and Angel 1932). Grey 1956:233 (synonymy; after Bertelsen 1951).

MATERIAL: Nine known females, 14.0–142.0 mm.

Holotype of *Caulophryne polynema:* BMNH 1930.2.7.1, 142 mm; "long line, in deep water," off Funchal Bay, Madeira; 1 February 1929.

NONTYPE MATERIAL: LACM 33923–1, 103 mm; *VELERO IV* Station 14962, 33° 10′N, 118° 31′W, 3-m IKMT, 1000 m wire, 0455–0943 hr, 10 February 1971. LACM 30619–3, 32.0 mm; *VELERO IV* Station 9903, 29° 30′N, 118° 54′W, 3-m IKMT, 0–834 m, 2315–0515 hr, 7 August 1964. LACM 32772–1, 24.5 mm; *TERITU* Cruise Vanilla Fudge, Station 69.11.4, 22° 00′N, 158° 00′W, 3-m IKMT, 0–1150 m, 1225–1635 hr, 12 November 1969. LACM 35897–1, 14.0 mm; *TERITU* Station 74.5.7, 21° 20–30′N, 158° 20–30′W, 4-m IKMT, 0–1000 m, 1405–1650 hr, 25 May 1974.

IOS uncatalogued, 110 mm; *DISCOVERY II* Station 8275, 32° 01.4′N, 50° 33.5′W, RMT, 0–1000 m, 2339–0150 hr, 5 March

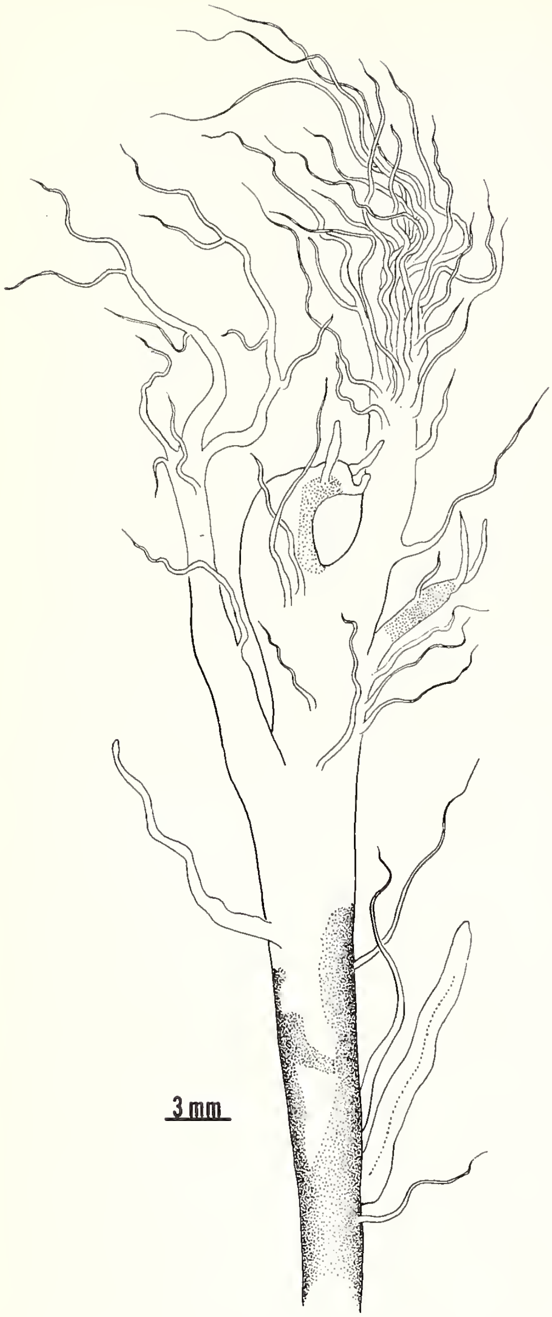


FIGURE 19. Esca of *Caulophryne jordani,* LACM 33924-1, 54.0 mm.

1973. IOS uncatalogued, 100 mm; *DISCOVERY II* Station 7856-50, 30° 03.7′N, 23° 00.2′W, RMT, 1000-1250 m, 0917-1317 hr, 5 April 1972. IOS uncatalogued, 11.5 mm; *DISCOVERY II* Station 7089-8, 17° 45′N, 25° 17′W, RMT, 900-1010 m; 0320-0659 hr; 13 November 1969.

ISH 3000/71, 44.0 mm; *WALTHER HERWIG* Station 510/71; 27° 18′N, 19° 44′W; CMBT-1600, 0-2000 m; 1752-2151 hr; 20 April 1971.

DIAGNOSIS: In addition to differences in escal morphology (Figs. 17, 19, 21), *C. polynema* is distinguished from *C. pelagica* and *C. jordani* in having a greater number of dorsal fin rays (Table 1) and a highly filamentous illicium (Figs. 17, 19, 21). It is further separated from *C. pelagica* in having a slightly shorter illicium (Fig. 16), and from *C. jordani* in having more upper jaw teeth (Fig. 18).

DESCRIPTION: Illicium lightly pigmented along anterior margin (fully pigmented in 44.0 mm specimen), and bearing numerous, elongate (up to 71 percent of illicium length), translucent filaments, most of which arise from posterior margin; more than 50 filaments in specimens larger than 32 mm, reduced to approximately 10 in smaller specimens; esca consisting of a posterolateral appendage with a palmate (usually bilobed), opaque, distal tip, and a tapering terminal appendage with an opaque distal tip; escal appendages highly filamentous in specimens larger than 44 mm, number and length of filaments reduced in smaller specimens (most escal filaments lost in holotype, see Regan, 1930:193, fig. 2; Fig. 21).

Total number of teeth in lower jaw 19-32, in upper jaw 30-45; vomerine teeth 1-3; D. 19-22, A. 17-19, P. 15-18 (Fig. 18, Table 1).

Measurements in percent of SL: longest tooth in lower jaw 5.6-9.5; longest dorsal ray 70-155; longest anal ray 60-151; illicium 16.0-32.1 (Fig. 16).

Rest of characters as for genus and family.

DISTRIBUTION: Five specimens of *C. polynema* have been collected from the eastern north Atlantic Ocean as far west as approximately 50° W. Four additional records are known from the eastern north Pacific: two from Hawaii and two from off southern California. The 100 mm IOS specimen from the eastern north Atlantic was captured with a closing trawl between 1000 and 1250 m (Fig. 24).

COMMENTS: *Caulophryne polynema* was separated by Regan and Trewavas (1932:100) from the other species because of its higher number of dorsal and anal-fin rays. Bertelsen (1951:36) however, noted that the high number of fin rays in caulophrynids (compared to other ceratioids) has such a large individual variation (D. 14 to 22, A. 12 to 19) that "we can scarcely attach much weight to this character." The greater amount of material available now indicates that despite this variation within the genus, fin-ray counts are of significant taxonomic importance. *Caulophryne polynema* can nearly always be separated from its congeners by its greater number of dorsal and anal-fin rays (see Key, Table 1).

Caulophryne species

Figures 16, 18, 22, 23

LACM 36025-1, female, 98.0 mm with parasitic male, 12.0 mm; *ALPHA HELIX* Southeast Asian Bioluminescence Expedition Station 37, Midwater Trawl 22, 4° 56′S, 129° 26′E, RMT-8, 0-2000 m, 0320-0530 hr, 12 April 1975.

DESCRIPTION OF FEMALE: Illicium unpigmented with approximately 30 elongate (up to 25 percent of illicium length), translucent filaments along entire length, those on proximal half of illicium arising from posterior margin; esca, a tapering appendage bearing numerous simple filaments and four highly branched lateral appendages: three, more proximal in position, one, more distal; opaque areas absent (Fig. 22).

Gonads well developed (right ovary, 22 mm long or 22.4 percent of SL, containing numerous eggs approximately 0.3 mm in diameter).

Total number of teeth in lower jaw 14, in upper jaw 22;

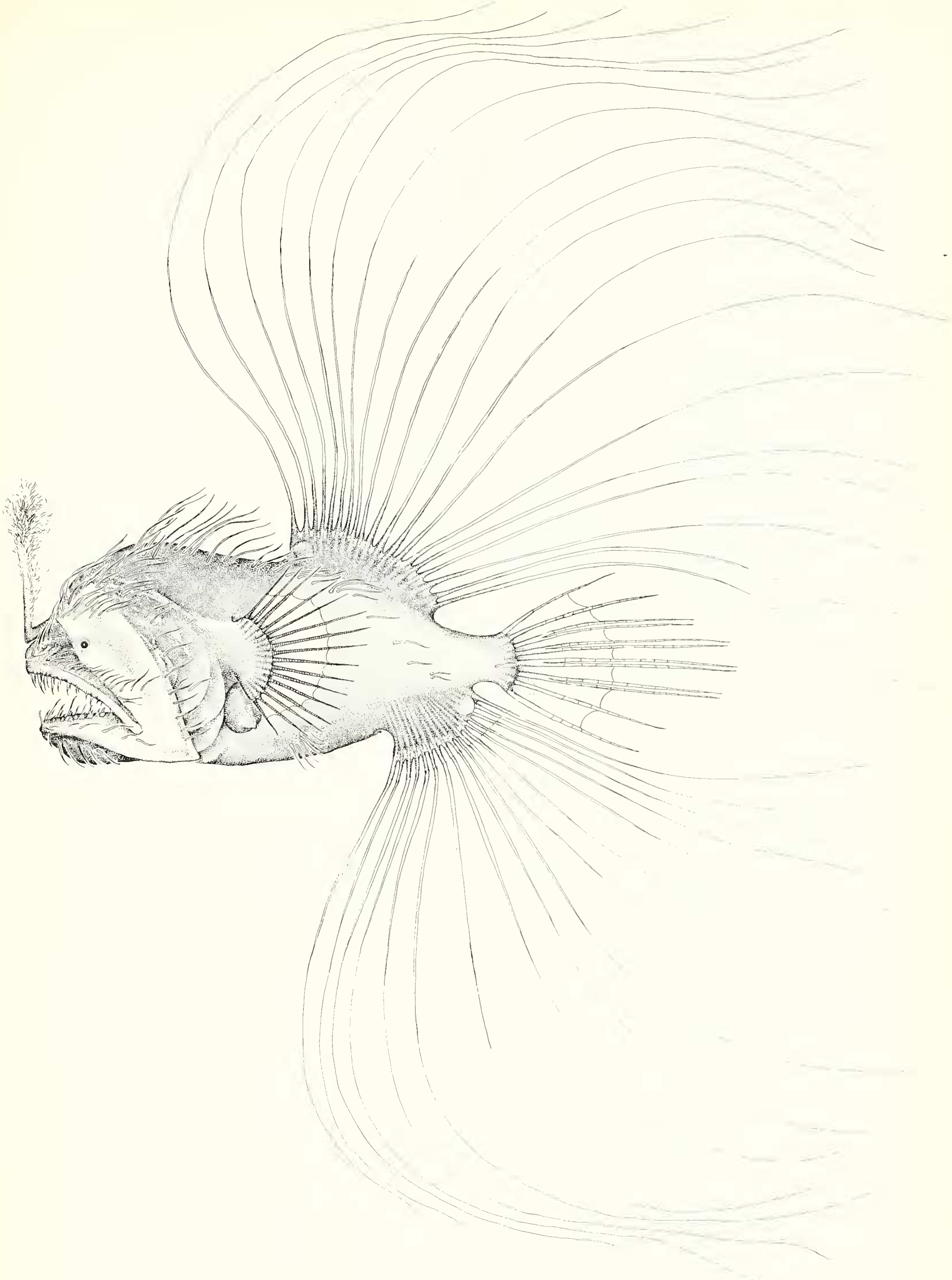


Figure 20. *Caulophryne polynema,* LACM 33923–1, 103 mm. Drawn by Elizabeth Anne Hoxie.

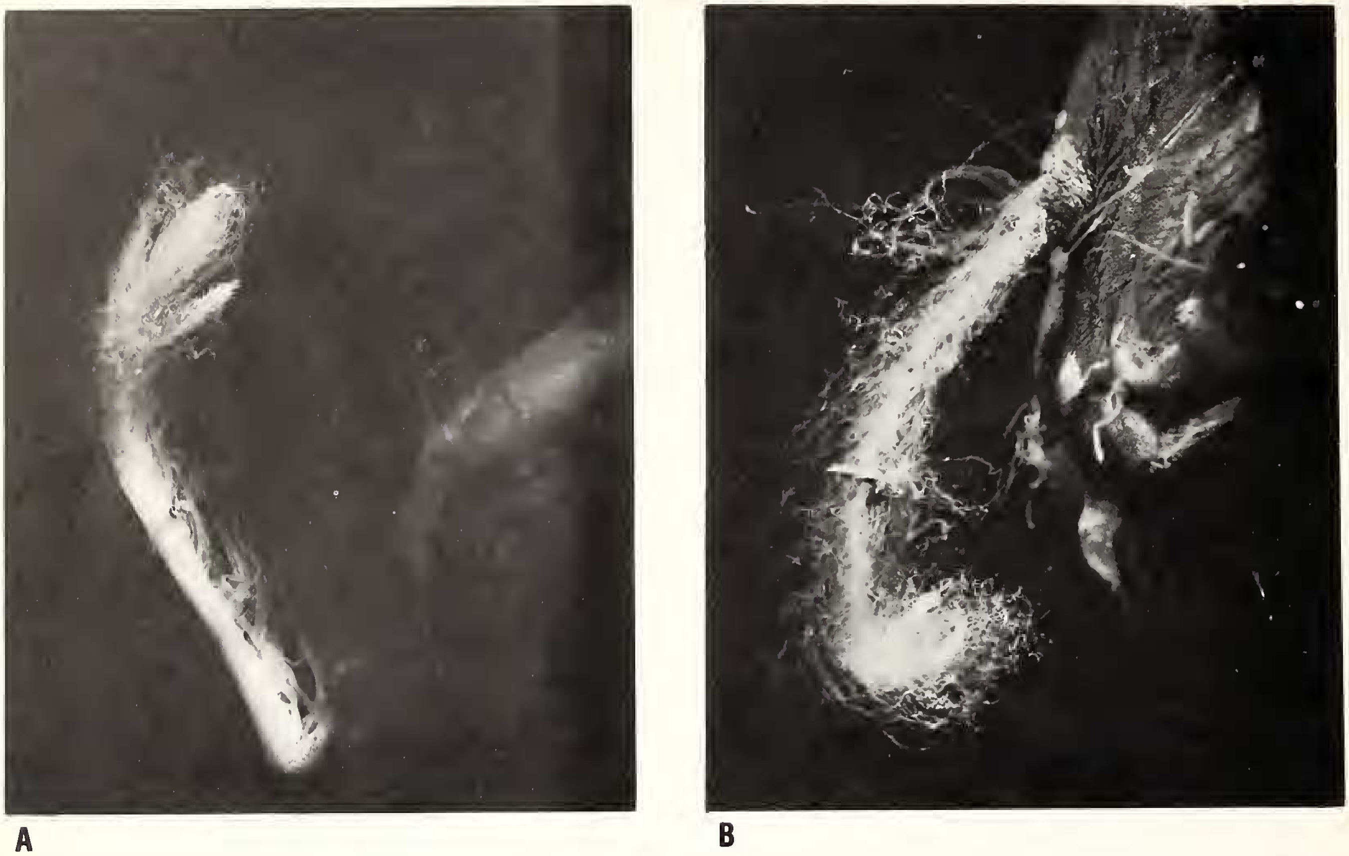


FIGURE 21. Escae of *Caulophryne polynema:* A. IOS, 100 mm; B. IOS, 110 mm. Courtesy of G. Brovard and E. Bertelsen.

vomerine teeth 1; D. 17, A. 15, P. 16–16 (Fig. 18, Table 1).

Measurements in percent of SL: longest tooth in lower jaw 9.2; longest dorsal ray 95+; longest anal ray 95+; illicium 27.6 (Fig. 16).

Rest of characters as for genus and family.

DESCRIPTION OF MALE: Upper and lower denticulars (Bertelsen 1951:21) embedded in an unpigmented, conical papilla on belly of female; passageway from outside into pharynx and out through gill openings retained (Pietsch 1976:790); eyes well developed; nostrils degenerate; gills developed; testes large (2.3 mm long, 19.2 percent of SL); dorsal, anal and pectoral-fin ray counts undetermined; pelvics absent; characteristic gelatinous envelope of larvae absent; entire head and body lightly pigmented (Fig. 23).

COMMENTS: This female and attached male cannot reasonably be placed within the material of any of the three recognized species of *Caulophryne*. The female has the elongate, branched escal appendages characteristic of *C. pelagica* but also the illicial filaments found only in *C. jordani* and *C. polynema* (compare Figs. 17, 19, 21, 22). The illicium appears to be slightly longer than that of *C. jordani* and *C. polynema*, but shorter than that of *C. pelagica* (Fig. 16). Jaw tooth counts are at the bottom of the range of variation for females of all species combined (Fig. 18). Finally, fin-ray counts compare best with *C. jordani* (Table 1).

The attached male (Fig. 23) represents the second example of sexual parasitism in the Caulophrynidae. It does not differ in any significant way from the previously described specimen (Bertelsen 1951:37, fig. 12).

Caulophryne setosus Goode and Bean 1896
NOMEN NUDUM

Caulophryne setosus Goode and Bean 1896:26*, 541, fig. 409.

COMMENTS: This name appears in a figure caption, and is entered in the list of plates and index of Goode and Bean's (1896) original description of *Caulophryne jordani*, without application to a description or type. This error was caught by Jordan and Evermann (1898:2735): "plate named *C. setosus*, by slip in proof reading." The name *setosus* also appears in the catalog of fishes of the National Museum of Natural History (S.J. Karnella, personal communication).

Caulophryne racemosa Monod 1960
NOMEN NUDUM

Caulophryne racemosa Monod 1960:687, fig. 80.

COMMENTS: This name appears in a figure illustrating stages of specialization of lophiiform pectoral radials. There is no application to a description or type. No doubt, Monod (1960) meant to refer to *C. ramulosa*. His figure was taken from Regan and Trewavas' (1932, fig. 58) illustration of the pectoral radials of the holotype of this nominal species.

DISCUSSION

The discovery of yet another new ceratioid genus brings the total number of genera based on females to 34. Although new forms continue to be described, it is unlikely that the total number of ceratioid species will increase significantly (Bertelsen 1951:28). In the last ten years 19 forms have been resurrected from synonymy or described as new (Pietsch 1969, 1972b, 1973, 1974a, b, 1975, 1978; Bertelsen 1973; Nolan and Rosenblatt 1975). During this same time, 28 nominal forms have fallen into synonymy, thus actually decreasing the number of recognized forms.

More so than any other ceratioid group, the caulophrynids exhibit a confusing mosaic of primitive and derived character states. Utilizing the variation found within the entire order Lophiiformes as representing the ancestral character pool for the Caulophrynidae, the following character states that describe *Caulophryne* are considered primitive:

1. frontal bones short, posterior in position, meeting on midline in front of supraoccipital (this is the condition of the frontals in lophioids and antennarioids; and, in addition to caulophrynids among ceratioids, the Neoceratiidae).
2. illicial trough absent (a narrow depression, usually running the full length of the cranium, is present in most ceratioids to receive the pterygiophore of the illicium; it is absent in caulophrynids and neoceratiids as well as in lophioids and antennarioids).
3. dorsal ceratohyal process present (this process is present in lophioids and antennarioids, but absent in all other ceratioids).
4. single epural present (no trace of an epural is found in any other ceratioid; lophioids and antennarioids, except for brachionichthyids, have one epural).
5. high number of median-fin rays (although *Caulophryne* exhibits a slight increase over the already high number of median-fin rays characteristic of lophioids and antennarioids, this probably represents a primitive condition over the greatly reduced median-fin ray counts of most other ceratioids; exceptions include some gigantactinids, neoceratiids, and melanocetids).
6. median-fin rays exceptionally long (like those of larval and young lophioids and antennarioids, but unlike any other ceratioid).
7. sexual dimorphism in the illicial apparatus of larval stages possibly absent (the 16 known caulophrynid larvae all have a well developed outer illicial rudiment, a structure normally found only in female ceratioids; the sex of these larvae cannot be determined from examining the gonads, but since it seems unlikely that only one sex is represented, Bertelsen (1951:31) suggested that the sexual dimorphism characteristic of other larval ceratioids, but absent in lophioids and antennarioids, might be absent in caulophrynids as well).
8. escal bulb absent (the esca of caulophrynids is not a bulbous, bacteria-containing organ as in other ceratioids but a tuft of filaments like that of many lophioids and antennarioids; in addition, Bertelsen (1951:31) stated that the illicium of caulophrynid larvae "is not globular or club-shaped as in most other female ceratioid larvae, but more finger-like as in certain antennarioid larvae.")
9. posteroventral coracoid process present (this process is also found in antennarioids; among ceratioids it is present in ceratiids, in the oneirodid genera *Spiniphryne* and *Oneirodes*, and present, but cartilaginous in gigantactinids).
10. pectoral fins exceptionally large, especially in larvae and young (like those of larval and young lophioids and antennarioids, as well as larval gigantactinids among ceratioids; Bertelsen 1951:35, 148, figs. 11, 99, 104).
11. pelvic fins retained in larval stages (pelvic fins, well developed in all lophioids and antennarioids, are not present in larvae or adults of any other ceratioid).

Caulophrynids are considered derived in having the following character states:

1. parietals anterior in position, far removed from posttemporals and expanded laterally.
2. pterosphenoid absent (also absent in linophrynids and gigantactinids).
3. anterior maxillomandibular ligament absent (also absent in linophrynids, gigantactinids and neoceratiids).
4. dorsal hypohyal reduced (absent in *Gigantactis*).
5. hyoid apparatus narrow and elongate (similar in linophrynids, gigantactinids, and neoceratiids).

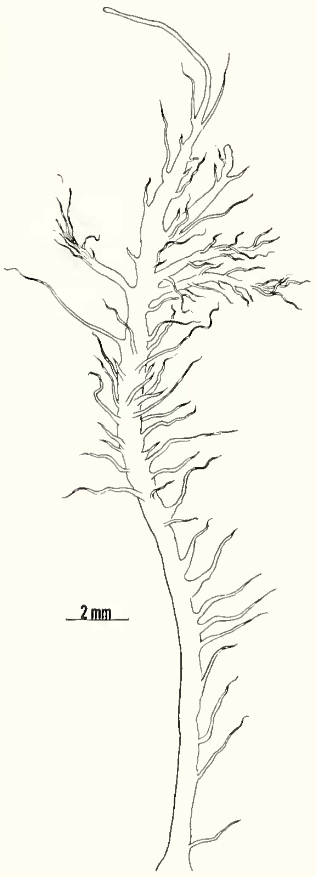


FIGURE 22. Esca of Caulophryne sp., LACM 36025–1, 98.0 mm.

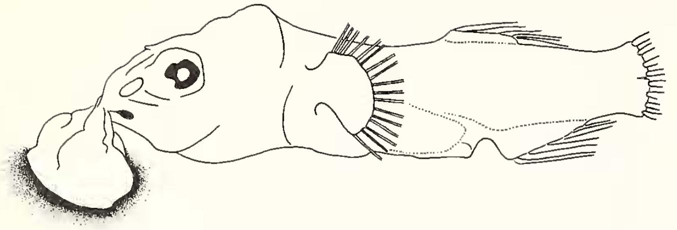


FIGURE 23. *Caulophryne* sp., parasitic male, LACM 36025-1, 12.0 mm.

6. opercular bones reduced (as are those of linophrynids, gigantactinids, and neoceratiids).
7. hypobranchials and basibranchials absent (all hypobranchials are absent in linophrynids and gigantactinids; hypobranchial II is absent, but a small hypobranchial III is present in neoceratiids; all basibranchials are absent in ceratiids, linophrynids, gigantactinids and neoceratiids).
8. caudal rays 8 (ceratiids also show a reduction in the number of caudal rays to 8; all other ceratioids have 9; neoceratiids occasionally have 10, Bertelsen 1951:159, table 36).
9. posttemporals reduced, overlapping pterotics and epiotics, but far removed from parietals and exoccipitals (similarly reduced in gigantactinids).
10. lower portion of cleithrum reduced to a slender thread of bone (similarly reduced in *Gigantactis*).
11. pectoral radial number reduced by fusion to 2 (all other adult ceratioids have 3 or more radials).
12. neuromasts of acoustico-lateralis system located at the tips of elongate filaments (this specialization is unique to caulophrynids; Regan and Trewavas 1932:23, 24, fig. 16C).
13. illicial filaments present in some species (also present in some species of *Gigantactis*).
14. males known to become sexually parasitic (Pietsch 1976:788; reproductive mode shared by ceratiids, linophrynids, neoceratiids, and the oneirodid genus *Leptacanthichthys*).

Due to the presence of a number of the primitive character states listed above (7, 8, 11), Bertelsen (1951:28) placed the Caulophrynidae "first in the suborder." At the same time, he argued that the Linophrynidae showed "such a highly specialized condition that they must be placed last." Since members of both these families are characterized by having parasitic males, Bertelsen's classification requires that this mode of reproduction evolved more than once. For unstated reasons, Greenwood, et al. (1966:397) implied a much closer relationship between the caulophrynids and linophrynids. Likewise, at the 1975 Annual Meeting of the American Society of Ichthyologists and Herpetologists in Williamsburg, Virginia, I reported finding numerous, derived character states shared by these two families as well as with the Gigantactinidae and Neoceratiidae. Ignoring all primitive character states at that time, I presented a phylogeny that argued for a monophyletic origin of sexual parasitism within a lineage derived from some oneirodid-like ancestor (Fig. 25; see also Pietsch 1976:791). This more detailed study of the Caulophrynidae has revealed a considerable number of additional resemblances (albeit, primitive states) to less derived lophiiforms (lophioids and antennarioids) that can hardly be ignored. That these primitive character states suddenly reappeared in a lineage that arose from an ancestor derived in all, is highly improbable; the importance of recognizing and utilizing primitive character states in phylogenetic analysis is apparent.

A return to Bertelsen's (1951) classification is proposed in

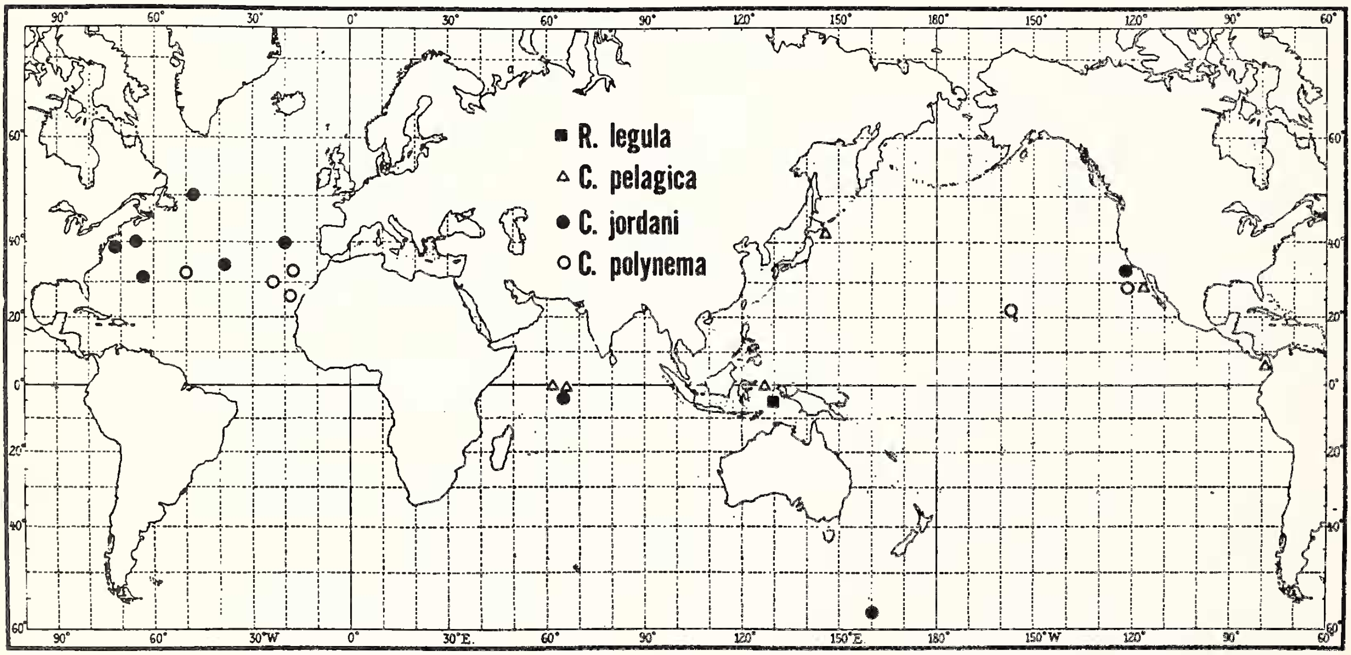


FIGURE 24. Known distribution of species of Caulophrynidae. A single symbol may represent more than one capture.

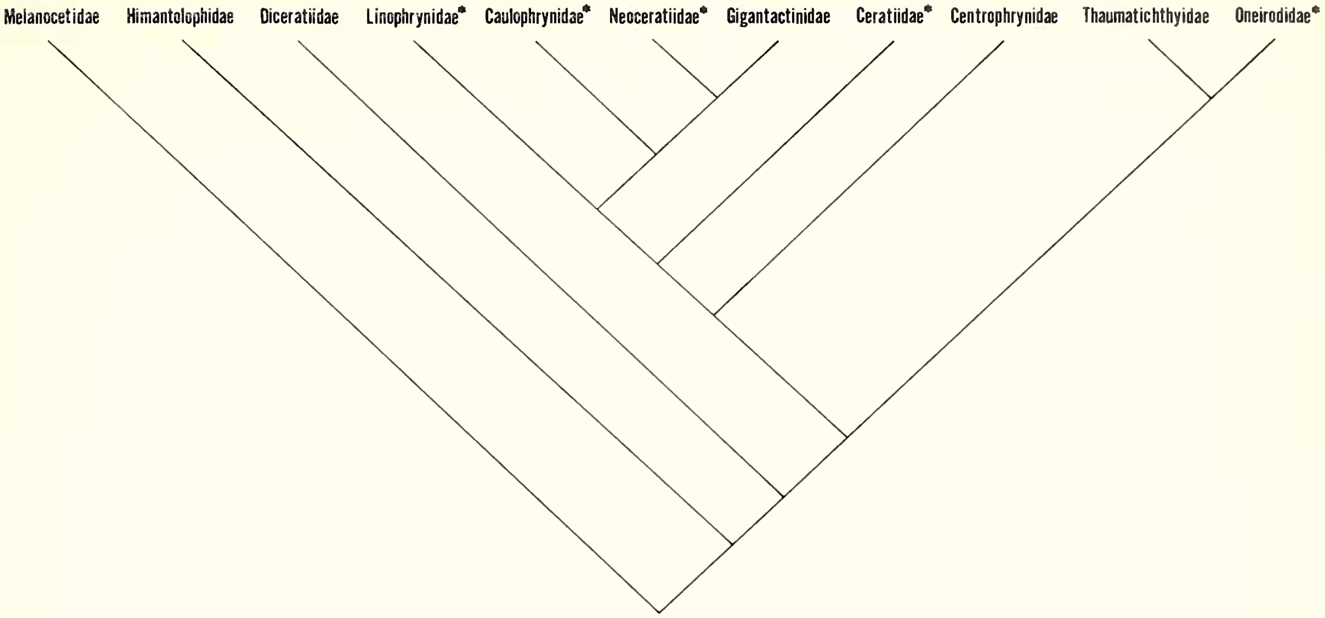


FIGURE 25. Phylogenetic relationships of families of Ceratioidei based on shared derived character states. Starred families contain species known to have parasitic males.

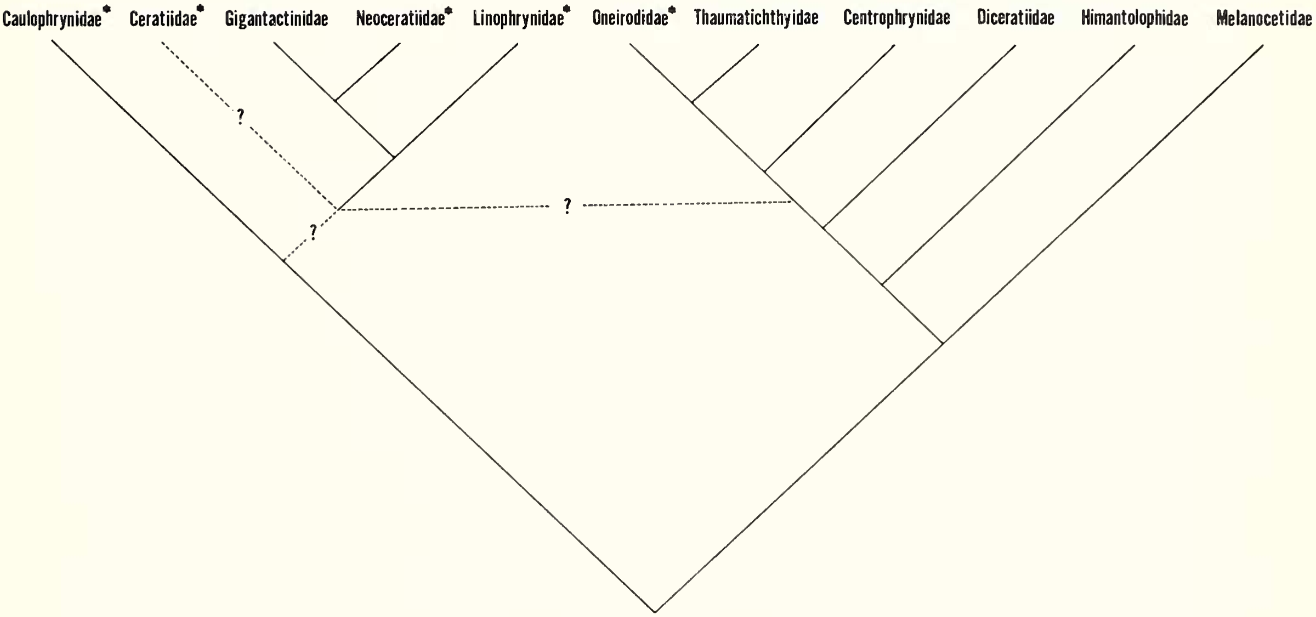


FIGURE 26. Phylogenetic relationships of families of Ceratioidei based on shared primitive as well as derived character states. Starred families contain species known to have parasitic males.

which the Caulophrynidae forms the primitive sister-group of the Melanocetidae, Himantolophidae, Diceratiidae, Centrophrynidae, Oneirodidae and Thaumatichthyidae (Fig. 26). The phylogenetic position of the closely related families Linophrynidae, Gigantactinidae and Neoceratiidae (and perhaps the Ceratiidae) is unclear. All share numerous derived character states among themselves and with the Caulophrynidae; but, most of these are either reduction states or loss of parts, conditions that are found in deepsea groups in general that could well be convergent in origin. This seems to leave two alternatives: either this assemblage is derived from a caulophrynid-like ancestor, thus forming part of a sister-group that is primitive to all other ceratioids, or it is derived from some oneirodid-like ancestor. Clarification of these problems must await further comparative studies; but, regardless of the phylogenetic position of the Linophrynidae and its allies, this interpretation, while recognizing the basal position of the Caulophrynidae, indicates a return to Bertelsen's (1951) view that sexual parasitism has evolved independently in at least two separate ceratioid lineages.

Three characters are available for interpreting intrafamiliar relationships:

1. median-fin ray counts. Within *Caulophryne* there is a trend toward an increase in the number of dorsal and anal-fin rays over the already high number of rays characteristic of lophioids and antennarioids. *Robia*, on the other hand, has a greatly reduced number of median-fin rays. The extremes of these opposite trends are both considered derived character states.
2. illicium length. Elongation of the illicium is a trend found in several other ceratioid groups (Pietsch 1972b, 1974a, b, 1975). The short illicia of *Caulophryne* species is a primitive condition; the extremely elongate illicium of *Robia* is derived.
3. illicial filaments. Within other ceratioid groups there is a trend toward an increase in morphological complexity of the illicial apparatus (Pietsch 1972b, 1974a, 1975). Filaments present along the length of the illicium of *C. jordani* and *C. polynema* (absent in all other ceratioids except for some species of *Gigantactis*) is considered a derived state.

This character analysis indicates that *Robia*, with its greatly reduced median-fin ray counts and extremely elongate illicium, is the more derived of the two caulophrynid genera. *Caulophryne pelagica* has a longer illicium than its congeners, but is considered the least derived member of the genus, having the lowest median-fin ray counts and lacking illicial filaments. *Caulophryne jordani* and *C. polynema* appear to be more closely related to each other than either is to *C. pelagica;* both exhibit an increase in the number of median-fin rays and share the presence of illicial filaments. *Caulophryne polynema* is the most derived member of the group having the highest median-fin ray counts and the most complex illicial structure.

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